ESTIMATION OF GENETIC PARAMETERS AND RESPONSES IN SELECTION FOR LITTER SIZE IN PIGS

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ABSTRACT

A large body of data from a single nucleus herd was used to investigate non-genetic and genetic sources of variation mainly as affecting litter size (LS) in pigs. Of particular interest were the effects of rearing treatment on gilts subsequent performance. Rearing treatment had a small negative effect on subsequent LS although not significant ($P>0.05$) due to a large standard error. However, a significant effect was observed on days to 90kg. Yet no evidence of bias on genetic parameters for LS from maternal (fraternal or rearing) environmental effects were detected. Thus, daughter on dam regressions ($b_{d,D}$) gave good estimates of genetic parameters with small standard errors. Heritability estimates from paternal half-sib analyses agreed well with $b_{d,D}$ estimates. A pooled estimate for the heritability from $b_{d,D}$ for LS was 0.11 ± 0.01 with repeatability (pooled) of 0.14 ± 0.01 among parities. Only the genetic correlations of first with third and fourth parities for LS deviated substantially from unity.

Despite the low heritability, high rates of genetic change are predicted for LS using conventional selection methods. The highest rates are predicted from selecting males and females born to gilts on an index combining litter records on the dam, her full-sibs and half-sibs as well as on the full-sibs of the sire, his half-sibs and dam. Two records would be available on each relative. Rates of just under 1/2 a piglet per year of selection are predicted assuming a simple additive genetic model. As a percent of the mean basis this is substantially higher than the expectation for much more heritable traits. The loss in selection efficiency from possible

fraternal effects are small with family index. Continuous screening and breeding from 'hyperprolific females' is much less effective due to the time needed for each cycle of selection. A single cycle of the scheme can be effective in starting an improvement program for LS or a specialized dam line. Increasing the accuracy of selection through incorporating family information is preferred to increasing the number of individual records because of the reduction in genetic lag. High rates of response are also predicted from selecting females on a family index as before combined with two stage selection of males, on the same family index and then on progeny test results.

The extra economic response from adding all family information for LS to a selection index including growth and carcass traits for selection of general purpose stocks is small (less than 5 percent) for UK market conditions. However, the same index information used for selection of specialised dam stocks could bring about an increase in the economic response of 5 to 19 percent, which is worthwhile and is recommended.

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CHAPTER I. INTRODUCTION AND REVIEW

Ollivier and Bolet (1981) reported no response to selection after 10 generations of selecting pigs for larger litter sizes. This result led to a considerable amount of attention to the investigation of parameter values for maternal effects and the re-evaluation of selection strategies for this trait. Evidence of the renewed interest in the subject of genetic improvement of litter size in pigs is illustrated by the many reviews that have appeared recently in the literature (Van der Steen, 1983, Hill, 1982, Hill and Webb, 1982, Ollivier, 1982, Johansson, 1981, and Vangen, 1981). There are also several selection experiments in progress, or being initiated, whose main objective is the improvement of litter size in pigs (e.g. Johnson, Zimmerman and Kittok, 1983, Bichard and Seidel, 1982, Bolet and Legault, 1982, Tomes and Newman, 1982 and Rutledge, 1980). Thus, litter size as a trait in its own right continues to be of considerable interest.

Litter size is a component of sow productivity so it should be considered in defining selection objectives in a pig breeding programme. The value of selecting for litter size is some function of its net contribution to the economy of production and the expectations of response to selection versus that from environmental manipulation. Some guidelines covering the first two points are available in the literature and will be reviewed briefly here. The possibilities of environmental manipulation are of course, important but outside the scope of this thesis. Also, the view is taken here that new technology in this area will have greatest

impact on short term decisions. On a long term basis, Smith (1978) has clearly shown the accrued economic value of genetic improvement.

The main objective of this thesis is to re-examine selection alternatives for increasing litter size in pigs. In the first part, parameters likely to affect selection strategies are estimated. Following the derivation of these parameters and using other estimates from the literature, some selection schemes are analysed theoretically in terms of expected rates of genetic response to selection for litter size. Special account is taken of current concern about the consequences of maternal effects on selection response. Finally, the value of including litter size in selection programmes is studied, since it may be argued that litter size should not be seen in isolation but included in selection with other traits of economic importance.

I.1 Net Contribution of Litter Size to the Economy of Pig Production

In a broad context it is easily seen that the costs of housing, keeping and feeding the sows and boars in a herd are incurred irrespective of production. It follows that higher levels of sow productivity lead to a reduced share of overheads and hence increased levels of efficiency (profit or returns). However, the relative contribution of litter size to the economy of production is still argued around three main points:

1. Market product demand
2. Litter size versus other measures of sow productivity
3. Reproductive performance versus growth and carcass traits

I.1.1 Market Product Demand

The importance of market requirements on the definition of breeding objectives is clearly demonstrated by Dickerson, Tess and Bennet (1982) in Table 1.1. This table is the summary of the results from a simulated deterministic bio-economic model. As can be seen, this model predicts very high contribution of litter traits for general purpose lines marketed on a live weight basis. The highest contribution is, as expected , for maternal lines. Strikingly in the latter case, improvement of growth rate and reduction of body fat were expected to make a negative contribution to the economy of production. However, when marketing on the basis of lean carcasses much more emphasis on low body fat content and high growth rate seemed indicated.

As expected, litter size is of little or no importance as breeding objectives for specialised sire lines. Here again market requirements were very important on defining breeding objectives. The direction and absolute magnitude of emphasis indicated for low body fat content and high growth rate are similar to general purpose lines. Note that pig viability turned out to be a very important contributing factor to the economy of production irrespective of market requirements.

TABLE 1.1

Economic value per genetic standard deviation improvement of each trait for cost of live weight (W) or carcass lean (L) relative to litter size (NBA)[1] or litter viability (VIAB)[2] and for marketing at 100 kg (D10) or at 185 days (185). (From Dickerson, Tess and Bennet, 1982)

		Traits					
		Litter traits		Age at	Market targets		Empty body
Source[3]	Output	NBA	VIAB	Puberty	D10	185	fat
a.	W[4]	100	---		149	---	61
b.	W[4]	100	---		62	---	133
c.	W[4]	100	---		61	---	25
d:							
Purebred	W	100	152	66	7	---	-32
	L	100	151	62	4	123	204
Rotation crossing	W	100	158	64	20	---	-32
	L	100	158	62	22	133	218
Maternal crossing	W	100	101	66	-23	---	-24
	L	100	100	65	-21	38	117
Paternal crossing	W	2	100	0	15	---	-13
	L	2	100	0	21	103	143
Mean		9	85	200	185		36
Coef.Variation (%)		25	20	10	10		10
Heritability (%)		15	5	40	30		40
Units		pigs	%	days	days		%

1 Importance reduced 1/2 because of selection on dams' performance.
2 For mean viability of litter.
3 Sources: a. Smith (1964), b. Dickerson (1977), c. NSIF (1981) and d. Tess et al. (1982)
4 With different premiums for carcass leanness among sources.

I.1.2 Litter Size versus Other Measures of Sow Productivity

Sow reproductive rate is now widely used as the main measure of sow productivity. Usually expressed as pigs per sow per year (p/s/yr) it is a powerful statistic summarising levels of performance for several component traits. Yet, from an animal breeding point of view, it has the disadvantage of many other composite traits, namely that the optimum weightings are not given to each of the components. Furthermore, very few estimates of genetic parameters other than for litter size are available in the literature.

Bichard (1983a) has recently given an account of components of sow productivity. He shows that under modern management practices, pigs weaned/sow/litter is a major component of p/s/yr accounting for about 67% of the variation ($r=0.82$). Similar relationships had been shown by Teffene and Vanderhaegen (1975).

Pigs born alive/litter and pigs weaned/litter are also highly correlated. This together with the achieved levels for other components of sow productivity led Bichard (1983a) to believe that further gains in reproductive efficiency may have to be obtained by increasing litter size.

Appendix A1.1 gives a rough estimation of the expected impact of some components of sow productivity relative to the time a sow remains in the herd. Here again, it is clear that litter size alone has a very significant impact throughout the lifetime performance of a sow.

I.1.3 Reproductive Performance versus Growth and Carcass Traits

Moav and Hill (1966) showed that returns from increasing

reproductive rate follows the law of diminishing returns. Hence, the regression of profit on reproductive performance is non linear and dependent on the mean level of performance. This is probably true for most traits as, for example, Hill and Webb (1982) now argue the possibility that increased leanness in modern pigs might make selection for other traits like litter size relatively more attractive economically. At the centre of the argument for not including litter size as a selection objective has been the low heritability of litter size and the fact that it is expressed only as adult females. Growth and carcass traits, with higher heritabilities were considered susceptible to change at faster rates under mass selection. This was repeatedly the result of expected responses calculated for alternative selection schemes (Smith, 1964, Moav and Hill, 1966 and Elsen and Sellier, 1978). This view was subsequently reinforced by the work of Clarke and Smith (1979) who introduced economic calculations to conclude that benefits would be small from including litter size as a selection objective.

I.2 Expected Response to Selection for Litter Size in Pigs

Expectations for the genetic possibilities of improving litter size come from two main sources: firstly, theoretical considerations and secondly experimental evidence. Theoretical considerations enter into the discussion of breeding programmes and some of the relevant literature will be reviewed briefly under each individual case studied in the second part of this thesis. Two critical elements (although not entirely independent) in defining selection strategies are the underlying genetic model and parameter estimates. A simple additive model is usually the first choice.

However, maternal effects are common in most domestic animals (see review by Robison, 1981) and recently considered of relevance for litter size in pigs. If such effects exist, they can affect the choice of selection plan. So, in this section, the evidence for maternal effects is first discussed followed by a summary of literature estimates of genetic parameters for litter size.

I.2.1 Maternal Effects on Litter Size in Pigs

Falconer (1955) observed in an experiment that litter size in mice responded to between full-sib family selection at a fairly high rate (realised heritability 0.24). In contrast, zero daughter on dam regressions were estimated from the unselected control population. This led Falconer (1965) to propose a model explaining the unexpected results with a negative environmental relationship ($\hat{m}$) between daughters and dam's litter size. The contribution of maternal effects to the daughter-dam covariance had been considered theoretically by Kempthorne (1955). A more generalized treatment of the problem by Willham (1963) showed how maternal effects contribute to the covariances of different groups of relatives. The variance components for Willham's model are difficult to estimate as illustrated by Thompson (1976) and require elaborate experimental designs as those of Eisen (1967). This has probably favoured the adoption of Falconer's model in pig literature related to maternal effects. Covariances amongst most relatives for Falconer's model are given by Thompson (1976).

Several reports of maternal effects in pigs have appeared in the literature. Rathnasabapathy, Lasley and Mayer (1956) reported experimental results showing that an increase of 0.127 and 0.045 ova

were expected for each pound increase in weaning weight and in 154 day weights respectively. No similar effect was observed for litter size (negative relationship but not significantly). Maternal effects were not discussed directly. Later, Urban, Shelby, Chapman, Whatley and Garwood (1966) observed a non linear relationship between a dam's litter size and her daughter's. They also pointed out the similarity of these observations with Falconer's (1955) results. Apparently little activity followed these early findings until a series of reports by Robison and colleagues (reviewed by Robison, 1981). Initially Revelle and Robison (1973) observed significant non linearity in the daughter on dam regression for litter size in pigs. Also the estimate of heritability from grand daughter on grand dam regression was over twice as large as the daughter on dam estimate although not significantly different from zero. They further observed that daughter on dam regressions estimated within groups of dams with small, average and large litter sizes were (+), (0) and (-). They concluded that these observations were evidence of negative maternal effects on litter size.

Nelson and Robison (1976) reported results of an intervention experiment where litter size had been standardised at birth to litters of 6 or 14 piglets (rearing treatment). At weaning, females raised in litters of 6 were significantly heavier. At farrowing the same females had a significant advantage of 1 corpora lutea and 0.88 in litter size ($P<0.01$) despite considerable differences between replicates. These results lead directly to an estimate of a maternal effect ($\hat{m}$) for a post-natal environmental effect between -0.11 and -0.14.

In another more elaborate intervention experiment with

pigs, Van der Steen (1983) reported that gilts reared in large litters produced on average -0.48 piglets after correcting for oestrus numbers at insemination (-0.32 before correction). Differences were not significant ($P<0.39$) and interpretation of the results complicated. Among other things the halothane gene was segregating in the experimental population with an estimated effect of -1.28 piglets. However, the effective difference in rearing treatments was of 5.4 piglets leading to an estimate of $\hat{m} = -0.09$.

Several reports from analysis of field data followed the report of Revelle and Robison (1973). Vangen (1980) found (-), (+) and (-) heritability estimates within groups of small, average and large dam litter sizes respectively. Although none of the estimates were significant, this is in contrast with other reports (summarised in Table 1.2). From the same study grand daughter on grand dam estimates of heritability were over three times as large as daughter on dam estimates.

TABLE 1.2

Literature summary of signs of daughter on dam regressions within groups of dams with small, average or large litter sizes

Classification of Dams litter size			Reference
Small	Average	Large	
-	+	+	Urban et al. (1966)
+	0	-	Revelle et al.(1973)
-	+	-	Vangen (1980)

In an original approach to the problem, Alsing, Krippl and Pirchner (1980) split daughter on dam regressions according to whether the dam's litter record corresponded to the birth litter of the daughter or otherwise. They found that heritability estimates from birth litters were smaller than estimates excluding birth litter although the differences were not significant. The method should theoretically be quite powerful to pick maternal environmental biases on regressions. Alsing et al. estimated the true heritability of litter size to be 0.30 and the negative maternal effect $\hat{m} = -0.08$. However, the nature of the data (questionaire survey with data split among several farms) was far from ideal. In contrast, more recently, Lobbke, Willeke and Pirchner (1983) obtained higher estimates from birth litters than from non birth litters. Again, the analysis was not straightforward due to hormonal treatment of gilts and equalization of litters at birth. Table 1.3 gives a summary of the different literature reports of maternal effects on litter size in pigs.

I.2.2 Parameter Estimates

A distinction is often made between estimates for litter size recorded as total born or total born alive. However, few estimates of the genetic correlation between the two appear in the literature. The few estimates available are very close to one and indicate that the two measures are genetically very similar, Table 1.4, and no distinction is made between them in the thesis.

TABLE 1.3

Literature estimates of rearing treatment effects ($\hat{m}$) on litter size for gilts reared in large (H) or small (L) litters

	Rearing treatment			effect	Reference
	H	L	H - L	$\hat{m}$	
NM+	14	6	8		Revelle et al
LS	8.31	9.19	-0.88	-0.11	(1973)
NM	8.90	5.50	3.40		Rutledge (1980)
LS	10.71	10.50	0.21	0.06	1. before selection
NM	10.06	5.77	4.29		2. after 2 genera-
LS	10.19	11.30	-1.11	-0.26	tions selection
NM	12	6	5.4++		Van der Steen
LS	9.79	10.27	-0.48	-0.09	(1983)

\+ NM = number of litter mates
LS = subsequent litter size
++ realised difference

TABLE 1.4

Summary of literature estimates of the genetic correlation between litter size recorded as total born and total born alive

Genetic correlation	Reference
0.89	Legault (1970)
0.96 ± 0.33	Young et al. (1978)
0.97	Bolet and Felgines (1981)
0.99 ± 0.01	Lobke et al. (1983)
0.96 ± 0.04	This thesis

The heritability of litter size is one of the most estimated genetic parameters in pigs. The reason may be that most sow herds keep litter records. Field records have been the major source of large data sets in the past. Consequently, parameters have been estimated accross a wide range of environments with possible confounding of effects. Most of the reviews already cited contain summaries of the literature estimates. Van der Steen (1983) has summarised literature estimates from large data sets ranging from 3000 to 9000 records. All the estimates given are for European Large White and Landrace populations. A weighted average of these give a heritability of 0.10 for litter size. There is considerable variation in the estimates but this should be expected for a trait with low heritability and with the range of data sample sizes (Van Vleck and Henderson, 1961).

Even small values of maternal effects ($\hat{m}$) are expected to bias substantially heritability estimates from daughter-dam regressions. Therefore, Table 1.5 summarises paternal half-sib literature estimates from large data sets. Again, the average is close to 0.10 with only one large deviant (0.66 from Young, 1978).

The repeatability of litter size has consistently been estimated at about 0.15 (summarised by Strang and Smith, 1979). Genetic correlations betweeen different parities are much less frequently reported. Table 1.6 shows a compilation of literature estimates of genetic correlations. Also shown are some recent estimates of heritability for individual parities not found in other reviews. Estimates of heritability vary little about an average value of 0.10 across parities (one through four). In contrast, genetic correlations do vary considerably and probably reflect

problems of estimation for characters with low heritability as pointed out by Robertson (1959).

TABLE 1.5

Summary of paternal half-sib estimates of heritability for litter size in pigs

Reference	Number of litters	h^2	Comments
Legault (1970)	11 266	0.07	Large White
From Legault (1970) review			
-Korkman (1947)	5 150	0.11	LW and Landrace
-Lauprecht et al.(1953)	4 976	0.14	LR and Weidschwein
-Van Oers (1964)	7 605	0.13	Landrace
-Shelby (1967)	1 560	0.31	Duroc (full-sib estimate much larger than half-sib)
Strang and Smith (1979)	38 000	0.04	Large White
	35 000	0.07	Landrace
From Hill and Webb (1982)			
-Eikje (1973)	38 000	0.19	Landrace
From Van der Steen (1983)			
-Eikje (1970)	4 918	0.16	Above average herd
	5 938	0.12	Below average herd
From Johansson (1981)			
-Christensen (1980)	90 000	0.13	
Johansson and Kennedy (1982)	4 151	0.11	Large White
	8 816	0.06	Landrace
Young et al (1978)	2 095	0.66	
Willeke and Richter (1978)	2 535	0.06	
Brandt and Glodek (1984)	9 979	0.04	

TABLE 1.6

Literature estimates of genetic parameters for litter size among individual parities

Source of estimates		a	b	c	d		e
Parameter	Parity						
h^2	1	0.11	0.13	0.09	0.07	0.10	0.11
r_g	1,2	0.47	2.60	0.72	1.03	1.06	1.04
	1,3	0.80	1.30	0.48	1.01	1.03	0.50
	1,4	-	-	0.06	0.99	1.00	0.46
h^2	2	0.11	0.02	0.08	0.07	0.09	0.10
r_g	2,3	1.21	0.83	2.38	0.90	0.97	1.29
	2,4	-	-	0.58	0.84	0.97	1.15
h^2	3	0.08	0.12	0.02	0.06	0.09	0.14
r_g	3,4	-	-	1.99	0.70	0.91	1.06
h^2	4	-	-	0.11	0.08	0.07	0.16
Total litters		8 816	7 306	21523	6988	16516	11671
Breeds		LR	LR	LW	LR	Cross bred	LR+LW

a Johansson and Kennedy (1982)
b Lobke, Willeke and Pirchner (1983)
c Bolet and Felgines (1981)
d Vidovic (1982)
e This thesis

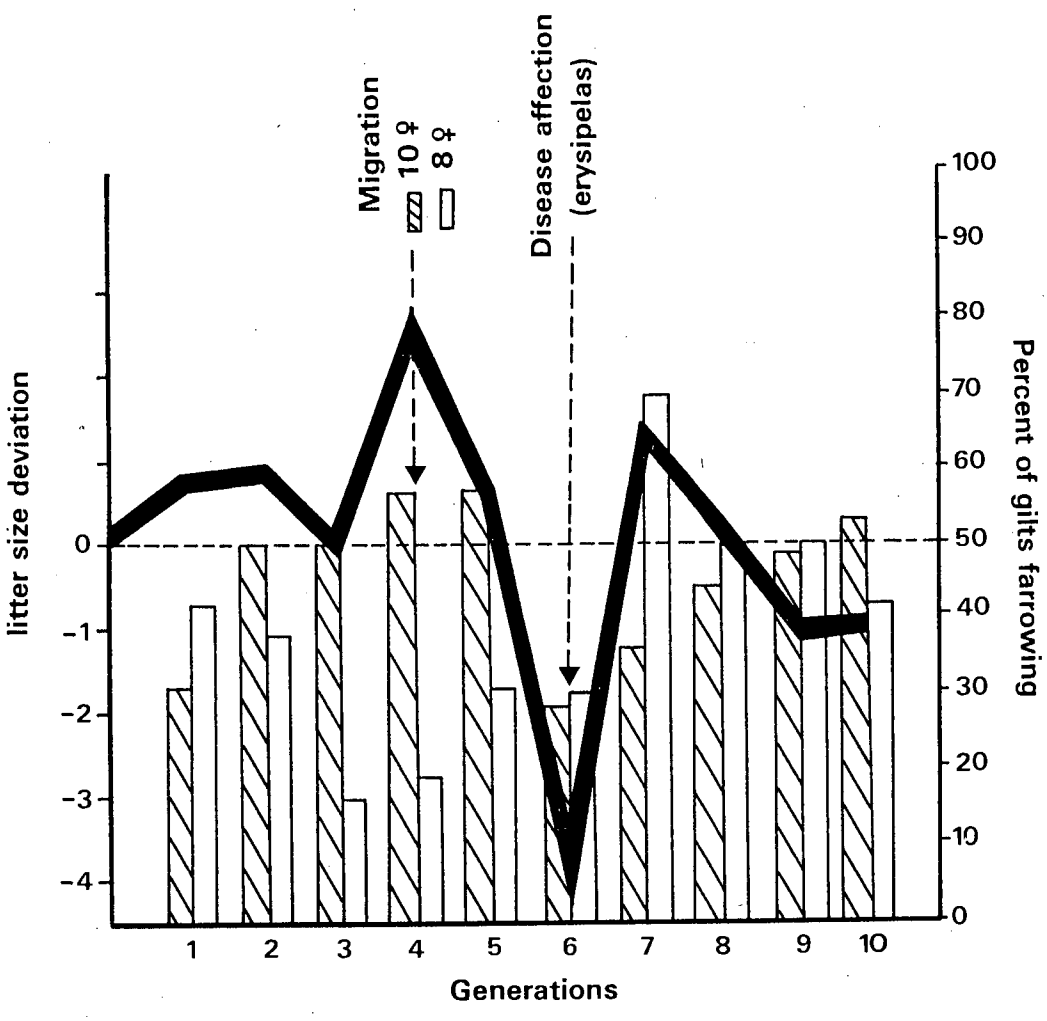
I.3 Response to Selection

The 10 year selection experiment reported by Ollivier and Bolet (1981) is the only one of its kind. The unsuccessful results are now widely quoted as evidence of poor expectations from this mode of selecting for litter size in pigs. Therefore, it deserves close attention. The experimental pig populations consisted of 120/50 females and 10/10 males for the selected/control populations respectively. The authors recognise that events out of their control lead to departures from the experimental design. The major cause of concern pointed out was the failure to obtain the effective number of litters expected (>50% each year). This situation forced the introduction of females from the 'exterior' in generation four. The origin and contribution of the newly introduced genes to the experimental population is not discussed. Clearly, however, the genetic make-up of the experimental populations could have been substantially affected with serious effects on the validity of conclusions drawn from the experiment. This and other factors are highlighted in Figure 1.1. More recently, Rutledge (1980) reported results of a two year selection experiment for litter size in pigs. Litter size appeared to have increased in the selected line but lines were small and the results to early to draw any useful conclusions.

Evidence for response to selection for litter size in pigs comes from Bichard and Seidel (1982). They screened a large single population of sows (nucleus and multiplier herds) and selected the top 1.7% based on the total number of piglets farrowed over time in four successive litters (equivalent to pigs/sow/year). After a

Figure 1.1

Litter size deviations between selected and controls and percent of gilts farrowing every generation. (from Ollivier's 1981 experiment)



selected line; 120♀. 10♂

control line; 50♀, 10♂

series of backcrosses to the selected sows, progeny were evaluated. The authors point out that they expected a genetic selection differential for litter size of between 0.7 and 1.1 piglets per litter although this was not the trait selected for directly. Subsequently, Bichard (1983a,b) has given evidence of the superiority of 'prolific' gilts over controls, both as purebreds and crossbreds. For example, an advantage for 'prolific' crossbred gilts over controls of 0.77 ± 0.26 piglets born has been reported (Bichard, 1983b). The genetic superiority of 'prolific' females appears to be maintained in subsequent parities . The final results for the trait selected (pigs/sow/year) are awaited. At this stage it is clear that litter size itself will probably have contributed substantially. There are indications that the average age at first effective service has increased by about 5 days among the 'prolific' gilts (Bichard, 1983b).

This experience shows a remarkable agreement with expectation and the assumptions behind this expectation are worth underlining, namely heritability 0.10, repeatability 0.15 and unity of the genetic correlation among parities.

Tomes and Newman (1982) also reported successful results from daughters of highly selected sows giving birth to sixteen or more live piglets (one record). But, the procedures are not clear and the numbers reported so far are small making it difficult to judge the reliability of the results.

Legault, Gruand and Bolet (1981) and Bolet and Legault (1982) reported the results of screening a large national population. A very significant increase in ovulation rate was

observed in progeny from the first backcross (grand progeny of 'hyperprolific' sows). However, a significant increase in litter size was only observed in second parity sows.

I.3.1 Indirect Response to Selection

Zimmerman and Cunningham (1975) selected pigs for increased ovulation rate for ten generations. The actual measurement taken was number of corpora lutea and for this they obtained a realised heritability of 0.42 ± 0.06 (Cunningham, England, Young and Zimmerman, 1979). No significant correlated response for litter size had been obtained by generation ten. The analysis of the last generation after a period of relaxed selection shows some correlated response for litter size (Johnson, Zimmerman and Kittok, 1984).

A distinction made between the measurement taken (corpus luteum) and the correlated response (ovulation rate) might be of some importance. Corner (1921) found that he could account for 96.8% of corpora lutea from ova recovered from the fallopian tubes. However, Squiers, Dickerson and Mayer (1952) were only able to account for 80%. Similarly, Lasley (1969) was only able to recover 80 to 85% of the ova based on corpora lutea counts, and concluded that ova not recovered probably never leave the follicle and some are lost in the abdominal cavity. It is possible that selecting for increased corpora lutea could result in selecting for a pathological condition of the ovaries.

I.4 Conclusions

The relative contribution of litter size to the overall economy of pig production depends on the simultaneous consideration of many factors and an unequivocal answer is unlikely. However,

litter size is an important component of sow productivity. Diminishing returns from further improvements on leanness in pigs makes it worthwhile to re-evaluate the possibilities of litter size selection in pigs.

The literature evidence for maternal effects on litter size in pigs is sometimes contradictory and the size of the effects is inconclusive. Genetic variation for litter size in pig populations is apparent, giving an average estimate of $h^2 = 0.10$, but maternal effects could have biassed many of the literature estimates.

At present the experimental evidence on the efficiency of selecting pigs continuously for litter size is inconclusive. For this to change, experiments would need to be designed in a large enough scale. However, several reports of a single cycle of selection of very prolific sows (judged on several records) clearly indicate that litter size in pigs should respond to selection by conventional methods.

PART 1

PARAMETER ESTIMATES

CHAPTER II. NON-GENETIC AND GENETIC FACTORS AFFECTING LITTER SIZE

II.1 Introduction

There is some uncertainty about the importance of various non-genetic factors in affecting estimates of genetic parameters for litter size and other reproductive traits in pigs. The objectives of this chapter are to use a large unique body of litter recorded data from a nucleus herd, over several generations, to

1) Investigate the importance of non-genetic (environmental) sources of variation and examine their effects on genetic parameter estimates.

2) Estimate genetic parameters for litter size, free of any such non-genetic effects.

Two types of non-genetic effects will be considered. One deals with the effects of an individual's early reproductive experience on subsequent reproductive performance. These include age at breeding, parity effects, lactation length, number of piglets reared, and rebreeding intervals. Some of these, but not all, are normally included in data analysis to estimate repeatability and heritability.

The other type deals with possible effects of the maternal environment (both prenatal and post natal) on the progeny's subsequent reproductive performance. The main post natal effect of interest in this study is the rearing treatment (or fraternal) effect reported by Nelson and Robison (1976), that gilts raised in large litters have smaller litters than gilts raised in small litters. These effects would bias estimates of heritability from daughter-dam regressions, as proposed by Revelle and Robison (1973)

and Alsing, Krippl and Pirchner (1980).

A general description of the records available is given first. This is followed by a description of herd management procedures. The reproductive life of a female is listed with average age (and range) at each event. This is given in some detail for its relevance to the analysis, and also to the second (operational) part of the thesis. The general statistical procedures used are then outlined, and the detailed form of the data described. The parameter estimates derived are then presented with more details on the analysis and particular statistical models used. Finally the parameter estimates are discussed and their relevance to further developments considered, specially with regard to their use in the second part of the thesis.

II.2 Description of records

II.2.1 Source of records

The data consists of records from a large nucleus herd of purebred Landrace (LR) and purebred Large White (LW) pigs. The records were collected and kindly made available for analysis by the Pig Improvement Company, Fyfield Wick, Abingdon, Oxford, England. A summary of the numbers of records available is given in Table 2.1.

The herd was founded in 1962. Its early history, management and selection procedures are described by Swales (1975). The data for the current analysis were collected over a 10 year period, beginning in 1970. The two breeds were housed together and treated as a single herd but were bred pure. Continuous selection was practiced by selection index for a common economic objective.

TABLE 2.1

Summary of litter records available for analysis

Farms+	1
Breeds	2
Years	10
Sires	556
Dams	1658
Sows	4806
Litters	11671

+Pig Improvement Company nucleus herd.
Fyfield Wick, Abingdon

II.2.2 Herd Management

Most management procedures followed standard commercial practice. Because of the nature of the herd (nucleus), particular attention was paid to identification of animals and to accurate recording. A detailed description of the herd's management is not really possible (nor would it be relevant to the analysis) since it was continuously changing over the 10 year period. However, there were some management practices that affect some of the variables under study, particularly those related to reproduction. These are described briefly below.

Females

The reproductive life cycle of an average female entering the breeding herd is shown diagramatically in Figure 2.1. The vertical lines mark events ending some stage in the reproductive cycle. The numbers on top of the horizontal line show the duration in days of a particular interval. The numbers below the horizontal give the age of the female at each event. Figure 2.2 shows the range (± one standard deviation) about the average values. Note that the distributions about the average intervals may not be normally distributed. Some of the distributions are skewed to the left and some are both skewed and bimodal (see Figures 2.3 and 2.4) For example, the interval from weaning to first service (Figure 2.4) is marked by a peak soon after weaning and a second smaller peak 21 days later. This is because the oestrus is naturally synchronised by weaning and the interval between consecutive ovulations is 21 days.

Gilts were performance tested from 45 to 90 kg liveweight. At the end of test they averaged 161 days of age. Mating started at about 200 days of age. Conception was on average at 222 days of age and so first litters were born when gilts were on average 337 days old. Thus the minimum age at first mating was partly set by the average performance to 90kg. The average lactation was 23 days. Weaning was originally practiced at 28 days and changed to 21 days in the last 5 years of the period covered. Sows conceived their second litter on average 23 days post weaning. This was on average 8 days longer than the time taken for their third and fourth litters. Duration of lactation was to a large extent set by farm policy although governed by factors such as piglet growth and vigour

Figure 2.1

Calendar events of an average female in the breeding herd (numbers refer to days)

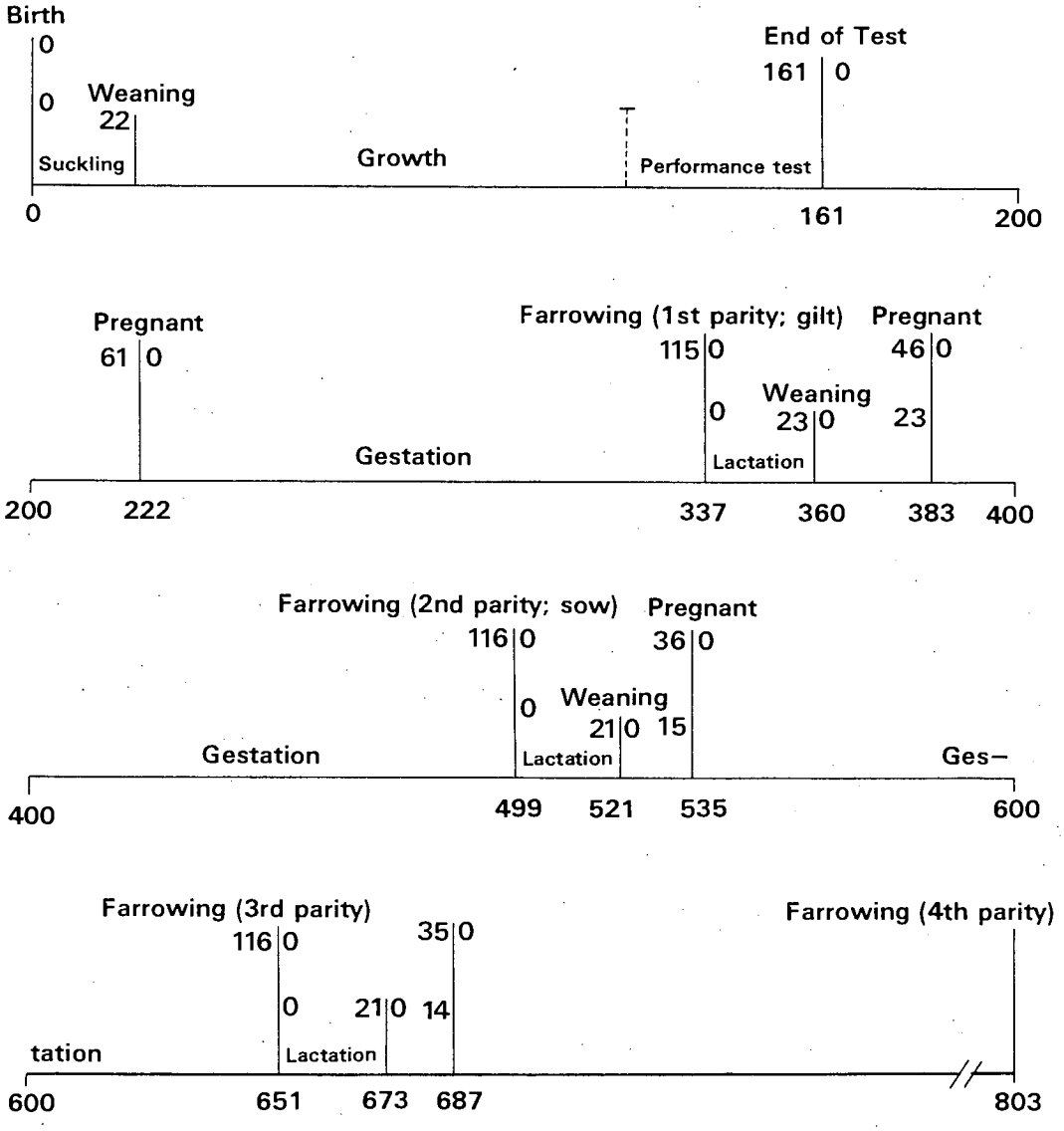


Figure 2.2

Variation about the main events in the life of a Female
in the breeding herd (numbers refer to days)

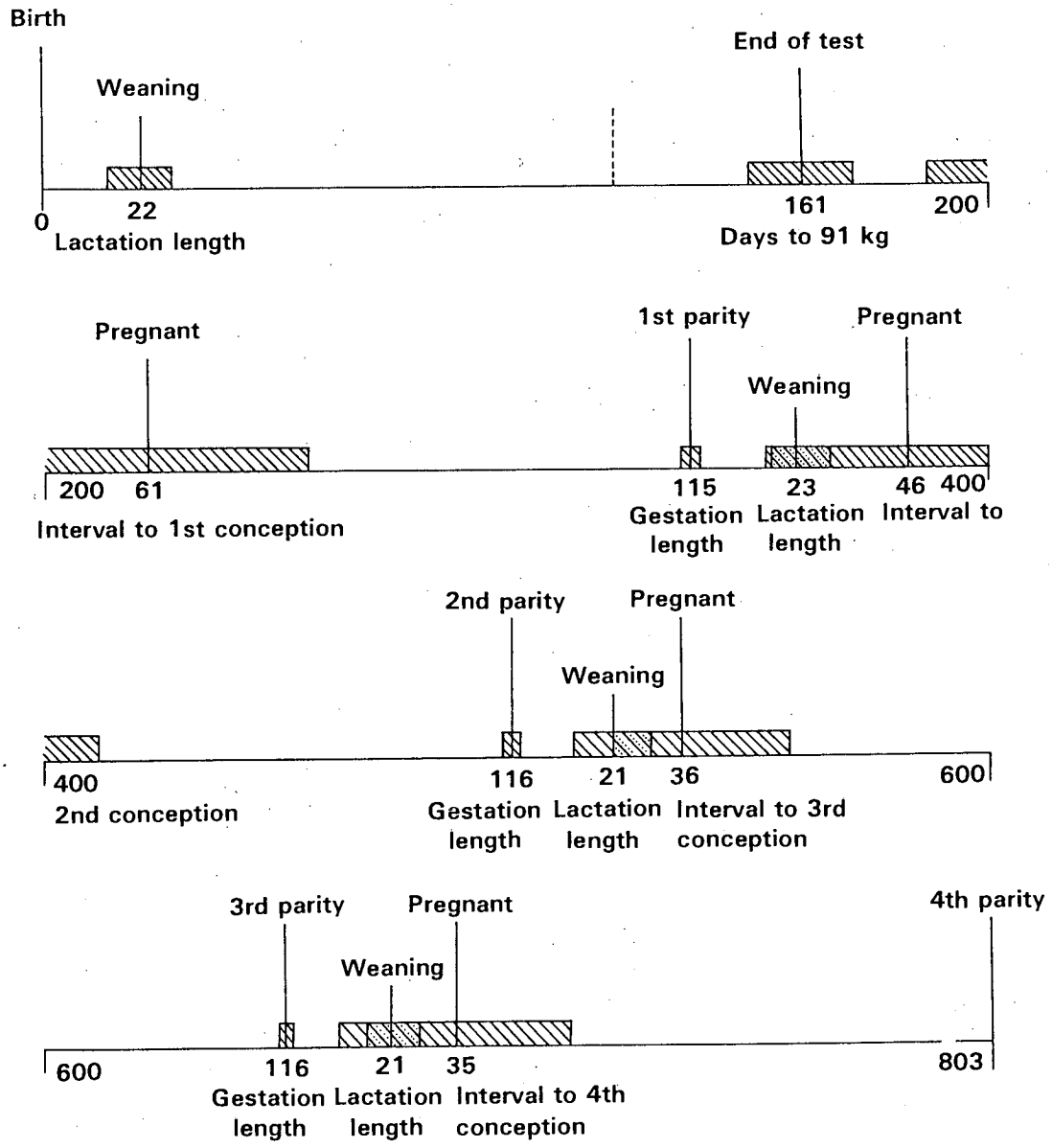
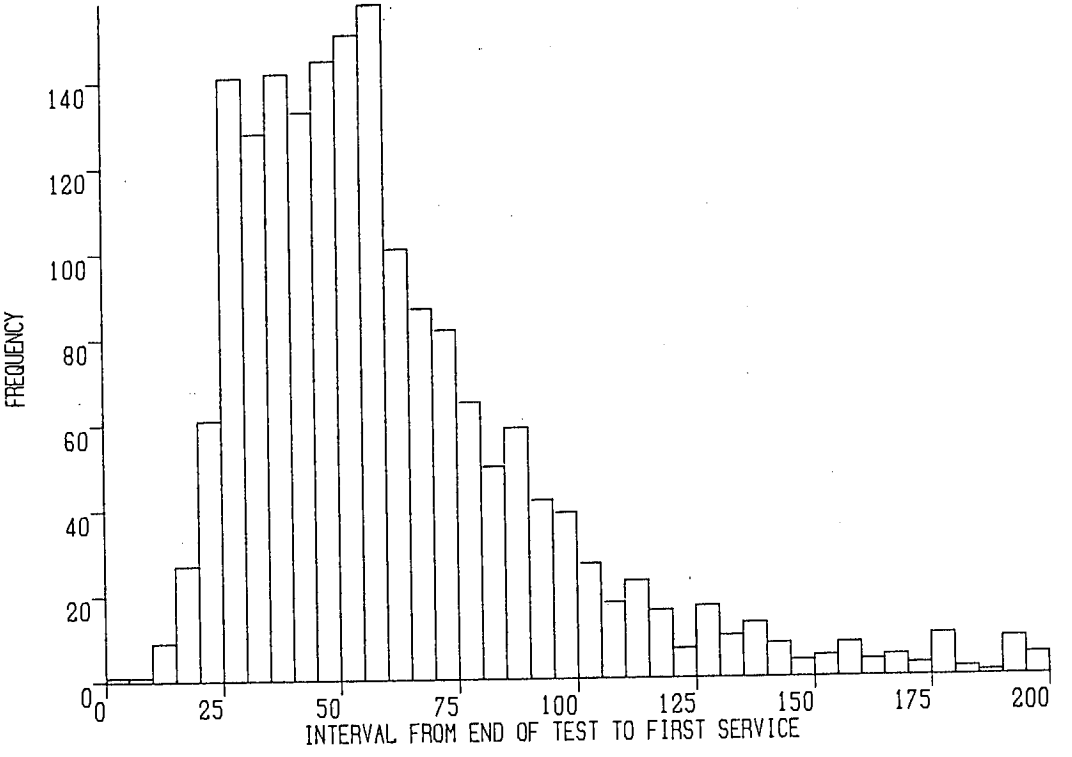


FIGURE 2.3 Distributions of days from end of test to first service and from first service to second service (gilts).



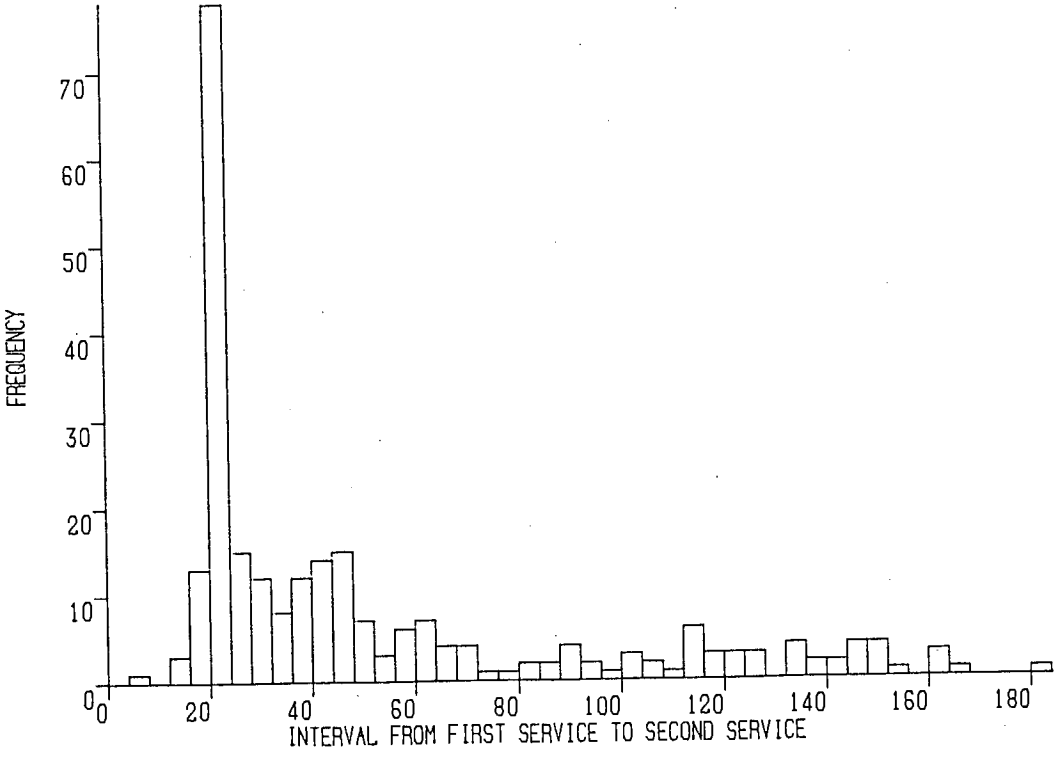
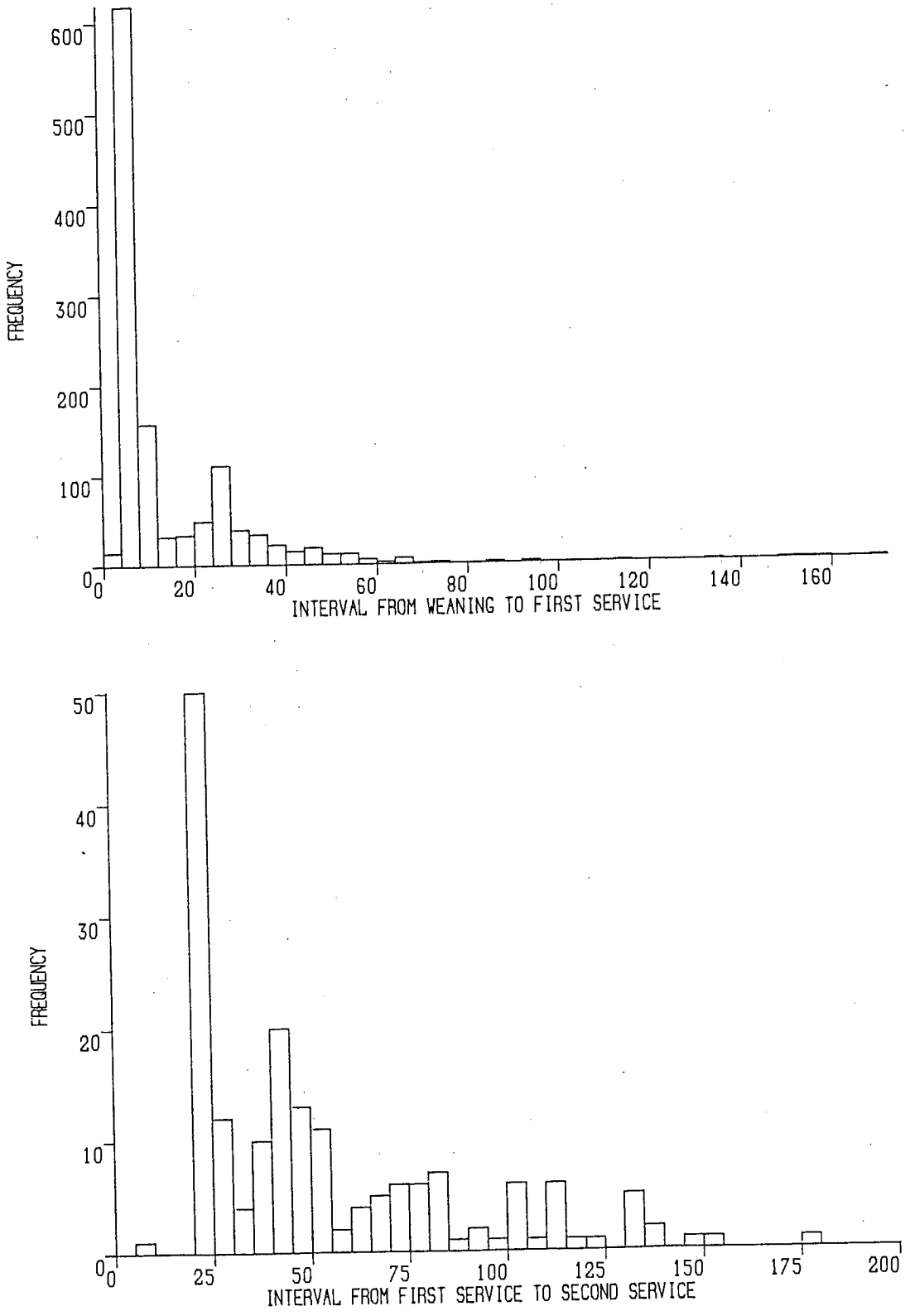


FIGURE 2.4 Distributions of days from weaning to first service and from first service to second service (second parity).



and the sow's milk supply. This in turn affected the interval to conception. Most females had their first litter within their first year of age, and had their second litter 162 days later on average. At this time their progeny from first litter would be at the end of their performance test. Thus two litter records on the dam (and on her contemporary sibs) would be available at the same time as the performance test records, so that all could be used together in selection (see Chapter 3).

Of gilts farrowed, 70% on average produced a second litter, 40% a third and 18% produced more than three litters. The biggest replacement took place after the second litter, to allow high indexing progeny to enter the herd. Most sows were given two consecutive services (12 hours apart) per oestrus. In general, those failing to become pregnant after their second oestrus were culled. Other culling criteria were not standard and were left to the discretion of the farm staff. Some small trials in artificial oestrus synchronisation, induction of parturition and other non-standard practices known to affect reproductive performance took place over the years but were not recorded.

Males

The young boars were mated soon after testing. The breeding policy was to replace boars after 20 services. They thus averaged 8-9 litters over a relatively short period.

Selection Criteria

Gilts were selected on an index combining age at 90kg and the sum of three ultrasonic measures of backfat. Boars were individually fed and food conversion was included in the index for

boars. No deliberate selection was practiced for reproductive traits.

II.2.3 Definition of traits

The main trait of interest in this study is litter size at birth. It was recorded both as number born and number born alive. Genetically the two traits are very highly correlated so either might be used. Hence litter size refers to number born alive, unless otherwise mentioned.

Records were also available on several other traits, both on production and reproduction. These are listed in Tables 2.2a and 2.2b, along with symbols, breed means and standard deviations.

TABLE 2.2a

Traits recorded on gilts, with symbols, breed means and standard deviations

Trait	Units	Mean		Standard deviation
		Landrace	L. White	
Number of records		1833	1821	-
Days to 91kg (D91)	kg	163.36	159.52	11.27
Backfat depth (CKL)	mm	49.59	49.60	5.91
D91 to conception	days	58.47	62.63	34.55
Gestation length	days	115.33	115.98	1.92
Lactation length	days	22.23	21.89	6.78
Litter size	pigs	9.81	9.77	2.67
Number suckled	pigs	8.44	8.02	2.63

TABLE 2.2b

Traits recorded on sows, breed means and standard deviations

Trait	Units	Mean Landrace	Mean L. White	Standard deviation
Second parity				
Number of records		1171	1221	
Weaning to conception	days	24.84	21.12	28.66
Gestation length	days	115.48	116.37	1.64
Lactation length	days	21.66	21.29	6.38
Litter size	pigs	10.02	10.04	3.28
Number suckled	pigs	8.56	8.49	2.62
Third Parity				
Number of records		676	662	
Weaning to conception	days	16.16	13.32	23.35
Gestation length	days	115.68	116.41	1.65
Lactation length	days	21.40	21.59	5.81
Litter size	pigs	10.69	10.92	3.17
Number suckled	pigs	8.72	8.94	2.35
Fourth parity				
Number of records		305	332	
Weaning to conception	days	14.39	13.72	23.83
Gestation length	days	115.84	116.41	1.73
Lactation length	days	22.13	22.43	6.22
Litter size	pigs	11.52	11.43	3.05
Number suckled	pigs	8.62	8.83	2.51

II.3 Statistical Methods

Most analyses were carried out by least squares procedures using a standard statistical package LSML 76 (Harvey, 1977). The procedure used was to fit the fullest model envisaged, to include all possible sources of environmental variation in the trait concerned. Non-significant ($P>0.05$) effects were then successively omitted from the model. The objective was to remove the maximum amount of attributable extraneous variation which would otherwise obscure the source of variation of interest. Effects of breed, year of farrowing, season of farrowing, parity (for litter traits) and interactions among them were tested. The interaction of year of farrowing and farrowing season was consistently significant ($P<0.05$) so year-seasons were used as contemporary groups. Different effects were investigated for the different traits as appropriate.

A summary of the distribution of litter size records among farrowing contemporary groups is shown in Table 2.3. For convenience, adjustments for the extraneous sources of variation were sometimes made before proceeding with other analyses. This was done in the genetic analysis because partitioning of the full data set into subsets was required or different sets of effects were involved in an analysis of covariance. The interpretation of some analyses requires an explicit representation of the statistical model used. In those cases the model is given either in the text or as a footnote to a table or an Appendix.

TABLE 2.3

Distribution of litter records among parities and contemporary groups (6 month farrowing periods)

Contemporary groups (6 months)	Parity 1	2	3	4
1	76	29	-	-
2	150	4	-	-
3	139	99	30	3
4	208	116	68	1
5	187	109	57	24
6	161	129	72	31
7	128	131	90	63
8	204	100	87	59
9	145	140	63	62
10	177	134	139	66
11	282	171	106	77
12	316	216	107	60
13	334	206	136	48
14	395	247	129	62
15	319	268	148	61
16	325	236	156	79
17	320	219	126	68
18	390	251	107	39
19	308	233	86	19
20	432	200	72	22
21	3	164	81	12
22	1	16	108	32
Total	4806	3343	1934	885
(percent)	41	29	16	8

II.3.1 Maternal environmental effects

Falconer (1981) made a distinction between two kinds of maternal effects. The first is when the phenotype of the mother affects the phenotype of the offspring for the same trait. This sort of effect will bias (through an environmental component) the covariance of offspring with dam, and also that among full-sibs. The second kind of maternal effect causes resemblance between offspring of the same mother but not between offspring and their mother. This sort of maternal effect is often described as common environmental effect. It is the first kind of effect that is considered here following the hypothesis of Revelle and Robison (1973), Rutledge (1980), Van der Steen (1983) and others. For convenience, Falconer's model (1965) for maternal effects is adopted (see Chapter 1 for reasons). Thus, maternal effects are defined as a (linear) function ($\hat{m}$) of the dam's phenotype. A more detailed description of the model is given in Chapter 4. The hypothesis is that individuals born or born and reared in larger than average litters have themselves smaller than average litters when bred.

(i) Bias on daughter on dam regression. Litter size can be expressed several times in a lifetime. So daughters and dam pairs can be subdivided into several sets, depending on whether the dam's litter record is the one in which the daughter was born, or otherwise. Following Alsing, Krippl and Pirchner (1980), two separate daughter (d) on dam (D) regressions (b) can be computed,

$$b_{d,D^*} = h^2/(2-\hat{m}) + \hat{m}$$

where D^* corresponds to the birth litter of the daughters, and

$$b_{d,D'} = h^2/(2-\hat{m}) + \hat{m}t$$

where D' is any other litter record of the dam and t is the repeatability of litter size estimated independently. Thus for the upper range of known parameter estimates for $\hat{m}$ (-0.15) and for a usual estimate of t = 0.15, this method should be powerful to detect bias on the daughter-dam regression. As in this case no distinction was made between prenatal and post natal effects, the two are confounded by this method of estimation. Also, as considerable crossfostering took place, the post natal component will be much reduced. Thus, for this data set, the method can only be a first approximation to the estimation of maternal environmental effects ($\hat{m}$). However, the method is useful because of its power to detect bias on daughter-dam regressions. The birth litter effect can be considered to be permanent or transitory. If it is permanent, all litter size records of individuals will be affected, otherwise, the effect could vanish with time. In the latter case the effect will be most noticeable on gilt records. Table 2.4 shows a summary of the number of daughter-dam pairs available among particular parity groups.

(ii) Rearing litter effect. Estimation of $\hat{m}$ as previously described depends on the validity of the genetic model. With a designed experiment it is possible to estimate $\hat{m}$ directly by fostering . Cross fostering is a common commercial practice and was used routinely in the PIC nucleus breeding herd. The low correlation (0.4) between birth litter size and rearing litter size gives some indication of the extent of cross fostering practiced. Thus it should be possible to estimate statistically a rearing litter effect independently. The following model was used in an attempt to

estimate the rearing litter effect:

$$y_{ijklm} = \alpha + B_i + P_{ij} + D_{ijk} + \bar{B}X_{ijkl} + B_{ijk} X_{ijkl} + e_{ijklm}$$

where

α is the overall mean

B_i is the effect of the i^{th} breed

P_{ij} is the effect of the j^{th} parity of dam within the i^{th} breed

D_{ijk} is the effect of the k^{th} dam in her j^{th} parity

$\bar{B}X_{ijkl}$ is a partial regression of a female's litter size on her own rearing litter size, averaged over all i,j and k groups

B_{ijkl} is the deviation of the individual's partial regression from the overall partial regression

e_{ijklm} are random errors

X_{ijkl} is the litter size corresponding to the l^{th} rearing group.

The regressions are fitted within dams in order to remove genetic variation among dams.

II.3.2 Genetic effects

Two basic forms of analysis were used for genetic interpretation.

(i) Regression across generations. These involved daughter on dam regressions and also grand daughter on grand dam regressions. The latter were considered, following Revelle and Robison (1973) to study genetic effects free of maternal effects, since a generation intervenes. However they are likely to have high standard errors because the genetic relationship of grand daughters and grand dams is 0.25. The regressions were used to derive estimates of the heritability for individual parities and also the genetic

correlations among parities. The records were repeated for each daughter and for each dam parity (when more than one parity was used in the analysis) (Kempthorne and Tandon, 1953). A summary of the total number of daughter-dam pairs available for individual parities is given in Table 2.4.

TABLE 2.4

Summary of number of records available for combinations of daughter dam parities and classified according to whether they correspond to birth litters or not

		Dam parity					
		1	2	3	4	Birth+ litter	Non-birth litter
Daughter parity	1	4112	3684	2805	1653	3668	8586
	2	2880	2589	1982	1218	2576	6093
	3	1678	1501	1144	714	1503	3534
	4	767	678	523	329	683	1614

+ Birth litter. Litter of dam in which daughter was born

Standard errors for the regressions were estimated as linear functions of independent components of variance which are themselves some known function of the heritability (h^2) the repeatability (t) and the variance (6^2). The method was suggested by R. Thompson (personal communication). In fact, for such low parameter values of heritability (0.10) and repeatability (0.15), the standard error of the regression co-efficients were approximately $\sqrt{1/n}$ where n is the number of daughter-dam pairs involved. Approximate standard errors for genetic correlations

were derived following Reeve (1955).

Daughter-dam regressions are expected to yield biassed estimates of heritability in the presence of maternal effects. Detection of such bias was one objective of this study. On the other hand, in the absence of maternal effects or adjustment for them, it can be seen from the summary in Table 2.4 that with the large numbers of pairs involved, the data set is expected to yield heritability estimates with low standard errors, in particular for first and second parities.

(ii) Analysis of covariance among collateral relatives. These analyses involved hierarchical analysis of variance and covariance to obtain paternal half-sib estimates of heritability and genetic correlations. More detailed procedures and models involved are shown in Appendix A2 in table form, together with the relevant text. Standard errors were estimated as linear functions of the variance and covariance components (Becker, 1975).

A summary of the distribution of family groups for different parity records is given in Table 2.5 and the average family size is given in Table 2.6. Numbers fall considerably after second parity. This increases the probability of obtaining negative between-group components of variance (see Gill and Jensen (1968) and Hill and Thompson (1978)). However, paternal half-sib analyses are expected to yield unbiassed estimates of heritability and so should provide some check on any biasses in daughter on dam regression estimates. Hill and Nicholas (1974) comment on the rationale for drawing conclusions from such comparisons.

TABLE 2.5

Distribution of family size for records corresponding to different parities

Family	Size	Parity 1	2	3	4
Paternal half-sibs	1	87	102	116	139
	2-4	152	183	221	158
	5-7	134	144	100	34
	8-10	93	66	20	4
	11-13	50	18	6	1
	14-16	27	12	3	
	17-19	10	3		
	>19	3			
Total	> 1	469	426	350	197
Full-sibs	1	2392	1951	1329	701
	2	691	463	234	75
	3	227	120	39	10
	4	66	20	5	1
	5	15	4		
	6	2	1		
Total	> 1	1001	628	341	86
Records		4806	3343	1934	885

TABLE 2.6

Summary of family sizes (larger than one) for different parities

Parity	Family	
	Full-sib (s.d.)	Half-sib (s.d.)
1	2.41 (0.70)	7.05 (4.11)
2	2.29 (0.58)	5.77 (3.25)
3	2.18 (0.43)	4.26 (2.39)
4	2.14 (0.38)	3.29 (1.72)

II.4 Results

II.4.1 Environmental effects of a sow's own reproductive experience

Rebreeding Intervals

Both breeds first conceived at about the same age although the interval from the end of test to conception was somewhat shorter for Landrace gilts (Table 2.7). Average days from weaning to conception at different cycles are shown in Table 2.8. Two features of interest are that from weaning, first parity sows took on average 8 more days to conceive than older sows. Although interactions between years and breed were present for particular parities, the Large White sows consistently averaged shorter times to conception so that by their fourth parity they had accumulated a seven day lead in farrowing age.

TABLE 2.7

Components of age at first farrowing by breed

Component	Breed	
	Landrace s.e.	Large White s.e.
Age at 91kg (D91)	163.4±0.9	159.5±0.9
Days from D91 to conception	58.5±1.5	62.6±1.5
Gestation length	115.3±0.1	116.0±0.1
Age at first farrowing	337.2	338.1

TABLE 2.8

Average days to conception in different reproductive cycles by breed

Cycle ending (parity)	Lactation length		Days to conception		Accumulative Difference
	Landrace LR	Large White LW	Landrace LR	Large White LW	LR-LW
First	22.2±1.5	21.9±1.5	24.8±1.3	21.1±1.3	3.1
Second	21.7±1.4	21.3±1.5	16.2±1.2	13.3±1.2	6.4
Third	21.4±1.4	21.6±1.4	14.4±1.8	13.7±1.7	6.9

Previous reproductive experience seemed to have little effect on subsequent farrowing intervals. However, there was a significant correlation between lactation length and the number of piglets suckled (r=0.51), due to lactation length being increased by

approximately one day for each extra piglet suckled.

Repeatability estimates for rebreeding intervals from second parity onwards were 0.26 ± 0.02 and 0.14 ± 0.02 for Landrace and Large White breeds respectively (see Appendix A2.1 for ANOVA). Adjustment to a constant lactation length increased the repeatability estimates only slightly as shown in Appendix A2.1.

Litter size

The effect of parity on litter size is shown in Table 2.9. There was a sharp increase of about one piglet from second to third parity. Additional variation was explained by a within parity regression of litter size on farrowing interval. The regression was significantly non linear with litter size ceasing to increase over the longer range of farrowing intervals. The estimated least square means after correcting for variation in farrowing intervals are also shown in Table 2.9. When previous succesive farrowing intervals were fitted simultaneously, only the farrowing interval immediately preceding had a significant effect on litter size. Age at first mating had a significant effect on litter size of Landrace sows in their second parity. Partial regressions were non linear and in the same direction. Table 2.10 summarises the effects of previous farrowing experience on litter size at different parities.

The repeatability of litter size among all parities was higher for Large White than for Landrace 0.17 ± 0.02 and 0.11 ± 0.02 respectively (Appendix A2.2).

TABLE 2.9

Effect of parity on litter size. Least square means before and after adjustment for farrowing interval

Parity	1	2	3	4
Number	4799	3337	1932	885
Mean (unadjusted)	9.91a+	9.98a	10.95b	11.31c
Mean (adjusted)	9.79a	10.24b	11.17c	11.43c

+ Row means with same letter are not significantly different P<0.05

TABLE 2.10

Effect of previous farrowing experience on litter size at different parities. Sign of partial regression coefficients for linear (L) and quadratic (Q) terms

Parity	1		2		3	
Coefficients for partial regressions	L	Q	L	Q	L	Q
Previous farrowing experience						
Number of piglets born			+	+	+	+
Number of piglets reared			-	-	(+)	(-)
Farrowing interval	+	-	+	-	+	-

() Effect not significant (P>0.05)

II.4.2 Maternal environmental effects

Bias on daughter dam regression.

Heritability estimates from daughter-dam regressions for gilt records classified according to one of two groups are shown in Table 2.11. Pooled estimates of heritability when birth litter was excluded from the analysis were not significantly different (P>0.05) from estimates from regressions on birth litter only (0.10 ± 0.03 and 0.09 ± 0.02 respectively). The corresponding estimates when daughter records for all parities were analysed are also shown. As before, no significant difference is apparent between estimates from the two groups of regressions, 0.12 ± 0.02 and 0.10 ± 0.01 for birth litter and excluding birth litter respectively. Neither was there any significant difference when compared to the estimate from grand daughter on grand dam regression (0.10 ± 0.03) also shown in the same Table.

TABLE 2.11

Heritability estimates from daughter dam regressions when the dams' record corresponds to the daughters birth litter and otherwise

Source	Landrace	Large White	Pooled
First parity			
Birth litters	0.05±0.05	0.14±0.05	0.10±0.03
Not birth litter	0.06±0.03	0.11±0.03	0.09±0.02
All parities			
Birth litters	0.07±0.03	0.16±0.03	0.12±0.02
Not birth litter	0.08±0.02	0.12±0.02	0.10±0.01
Grand daughter on grand dam	0.10±0.04	0.11±0.04	0.10±0.03

Rearing litter effect

Estimates of rearing litter effects are shown in Table 2.12. There were no significant effects. The pooled estimate for the rearing litter effect on gilt litter size was -0.03 ± 0.12. When all parity records were considered, the estimate was -0.08 ± 0.08. However, rearing in larger litters had significant effects on age at 90kg ($P<0.05$) and on backfat thickness ($P<0.05$) at the end of test.

TABLE 2.12

Rearing litter effect on subsequent performance. Partial regressions of performance on rearing litter size

Breed	Landrace	Large White	Pooled
Performance trait regressed			
Litter size (gilts)	-0.06±0.18	0.00±0.17	-0.03±0.12
Litter size (all parities)	-0.16±0.13	-0.01±0.11	-0.08±0.08
Days to 90kg	0.89±0.58	0.64±0.56	0.77±0.41
Backfat depth (mm)	-0.36±0.35	-0.20±0.33	-0.28±0.24

Model: $y_{ijklm} = \alpha + B_i + P_{ij} + D_{ijk} + \bar{B}X_{ijkl} + B_{ijkl}X_{ijkl} + e_{ijklm}$

(see text for symbols)

II.4.3 Genetic effects

Heritability estimates and genetic correlations among parities

The previous analyses give some suggestion that the genetic parameters for the two breeds might be slightly different.

However, the differences are small and the pooled estimates are presented.

Rebreeding intervals and performance test traits

Heritabilities and genetic correlations among different parities were estimated from daughter on dam regressions. Many regressions gave negative estimates for the heritabilities. The genetic correlation estimates were particularly variable and are not presented.

Estimates of heritability for age at 90 kg and backfat depth are shown in Table 2.13. Paternal half-sib estimates are larger than those from daughter-dam regressions. Some confounding between environmental effects and sire components is possible due to the short period in which most sire's progeny were born.

TABLE 2.13

Heritability estimates from daughter - dam regressions and paternal half-sibs for the performance test traits

	Heritability estimate	
Source	Daughter-dam regression	Paternal half-sib
Age at 90kg	0.30±0.04	0.49±0.10
Backfat depth	0.41±0.04	0.58±0.11

Litter size

Pooled estimates of heritability and phenotypic and genetic correlations among different parities are given in Table 2.14. The genetic correlations among adjacent parities were close to unity but

those for first with third and with fourth parities were substantially lower. Heritabilities were lower for first and second parity, (0.11 ± 0.03 and 0.10 ± 0.04 respectively) than for third and fourth (0.14 ± 0.06 and 0.16 ± 0.11 respectively). However, standard errors were increasingly higher for third and fourth parities due to smaller numbers of daughter-dam pairs with both sets of litters.

TABLE 2.14

Heritabilities, genetic and phenotypic correlations+ among different parities for litter size

		Parity			
		1	2	3	4
Parity	1	0.11±0.03	0.17	0.17	0.16
	2	1.04±0.20	0.10±0.04	0.18	0.23
	3	0.50±0.22	1.29±0.22	0.14±0.06	0.23
	4	0.46±0.21	1.15±0.19	1.06±0.28	0.16±0.11

+ Heritabilities on the diagonal, phenotypic correlations above and genetic correlations below the diagonal

The pooled estimate of heritability across parities for litter size was 0.08 ± 0.02 in Landrace and 0.13 ± 0.02 in Large White, giving an overall estimate of 0.11 ± 0.01.

The heritability of litter size for gilt records was also estimated using collateral relatives. The pooled estimate of heritability for litter size from paternal half-sibs was 0.07 ± 0.06 for number born from and 0.08 ± 0.06 for number born alive. The

genetic correlation between number born and number born alive was 0.96 ± 0.04. Analysis of variance tables are given in appendices A2.3 and A2.4.

Some of the heritability estimates from sib analysis for other parities were negative due to negative sire components of variance. However, estimates were obtained for all parities individually from the unadjusted data. All the paternal half-sib estimates and full-sib estimates of heritability are shown in Table 2.15. As with the daughter-dam estimates, those for third and fourth parities were larger than for first and second.

TABLE 2.15

Components of variance and heritability estimates for litter size at different parities from a sib analysis on the unadjusted data

	Parity			
	1	2	3	4
Variance components				
Between sires	0.14	0.21	0.32	0.38
Between dams within sires	0.16	0.86	0.53	0.10
Within progeny	6.65	8.75	8.72	8.61
Heritabilities ($h^2 \pm se$)				
Half sib estimate	0.08±0.06	0.08±0.09	0.13±0.17	0.17±0.36
Full sib estimate	0.09±0.05	0.21±0.07	0.18±0.11	0.11±0.21

II.5 Discusion

The data set is unique in analysis of this kind. It is from a large, well recorded nucleus population with several generations under a relatively controlled (standard) environment. In common with most field data, compared with experimental data, it lacks power to answer some specific questions. However, most of the genetic analyses are useful and the parameters reasonably estimated, and confirm the low heritability of litter size. The data and analyses were less useful in resolving environmental factors which may affect the estimates. Splitting the analysis in the way suggested by Alsing, Krippl and Pirchner (1980) gave no evidence of bias on the daughter-dam regression. In fact the results were in the opposite direction. Arguably the inability to detect any bias could be due to normal practices of crossfostering in the farm. If so, prenatal effects must be small and the practice of crossfostering effective in eliminating any post natal effects. The statistical model used here to estimate the rearing litter effect $\hat{m}$ was appropiate but lacked power. Effectively, few points were left to estimate the regression so the estimates had large standard errors. Though neither of the estimates of $\hat{m}$ were significantly different from zero, they support reports of negative effects of rearing litter size (Revelle and Robison 1973). The significant effects ($P<0.05$) for age to 90 kg and backfat thickness agreed with early reports by Rathnasabapathy, Lasley and Mayer (1956) and others (reviewed by Johansson (1981). The inability to detect significant maternal effects on litter size in the PIC data gives confidence in the heritability estimates from daughter-dam regressions. These have

been estimated with very low standard errors due to the large number of pairs involved, a feature of the data set. Adding to this confidence are the very similar estimates from grand daughter on grand dam regressions as well as the paternal half-sib estimates. The full-sib estimates were predominantly larger than paternal half sib estimates from the unadjusted data. This could give some indication of environmental effects common to litter mates (c^2) but also could be due to dominance effects for this lowly heritable trait. Strang and Smith (1979) also reported full-sib estimates substantially larger than half-sib estimates. However, few full-sib estimates of heritability appear in the literature. Note that corrections to records would have little effect in removing litter (c^2) effects.

In this study, only the genetic correlations of litter size in first with third and fourth parities deviated substantially from unity. Vidovic (1982) reported genetic correlations among all four parities very close to one. Yet, there is considerable heterogeinity of estimates in the literature (see Table 1.6). The view taken here is that this reflects problems of sampling in estimation, as pointed out by Robertson (1959) rather than real differences. However, there is no reason in principle why the true genetic correlation could not depart from unity. Tartar and Bolet (1984) have considered this possibility and suggest constructing indices where each parity is treated as a separate trait. This is not difficult but does require good knowledge and confidence in parameters. Progressive culling of females on their previous performance, smaller numbers of litters for latter parities and the

low heritability of litter size will be a major problem in getting better estimates of the genetic correlations from field data.

From the results of this analysis and taking account of the literature, it is reasonable to conclude that 0.10 and 0.15 are good working estimates of heritability and repeatability for litter size. In particular, these average estimates should be used with some confidence for British Large White and Landrace populations due to the very close agreement between estimates from this thesis and previous ones from Strang and Smith (1979). Results from this thesis also suggest that maternal environmental effects ($\hat{m}$) of the sort described by Nelson and Robison (1976) may be of little importance under modern management practices.

PART 2

SELECTION SCHEMES

INTRODUCTION

In the second part of this thesis, several selection schemes are analysed. For the next four chapters, litter size is the sole objective of selection. Index selection using family information is first considered in Chapter III. Initially a simple additive model is assumed. Later some of the simplifications are dropped and maternal environmental effects included in the model. The consequences of ignoring such environmental effects on the family index are explored in Chapter IV. Next, the continuous use of a 'hyperprolific' scheme is analysed in Chapter V. Also, in this chapter, the special case of using a 'hyperprolific' scheme for foundation of specialized dam lines is evaluated. A progeny testing scheme for litter size with selection applied in two tiers is considered in Chapter VI. Finally, in Chapter VIII the rest of the economic aggregate genotype (for growth and carcass traits) is included in the index calculations. The value of litter size (including all family information) is considered in this context.

CHAPTER III. INDEX SELECTION. Simple additive model

III.1 Selection system

In selection for litter size in pigs, advantage can be taken of their early puberty and rebreeding rate. Thus both males and females can be selected and mated at 6 months of age. By this time their dams should have two litter records (at 12 and 18 months of age) on which selection can be based. The generation interval then is one year in both sexes, with all replacements taken from first litters and selected on two records of their dams. Ollivier (1974) has shown that this system of selection, with its rapid generation turnover, maximises the rates of genetic change in litter size in pigs.

The accuracy of selection of the replacements can be increased by including information from other relatives, using a selection index. In addition to the dam, records will also be available on her full-sibs and her half-sibs (dam family). There will also be information on the full-sibs, half-sibs and dam of the sire (sire family) of candidates for selection. Moreover, as noted above, two litter records should be available on all relatives in time for selection.

III.2 Selection herd

Consider a nucleus selection herd in which selection on litter size will be practised. Each sire will be mated at about 6 months and at 12 months of age to dams of similar ages producing on average 3 males and 3 females per litter. Breeding replacements will be chosen at six months of age, born from first litters but

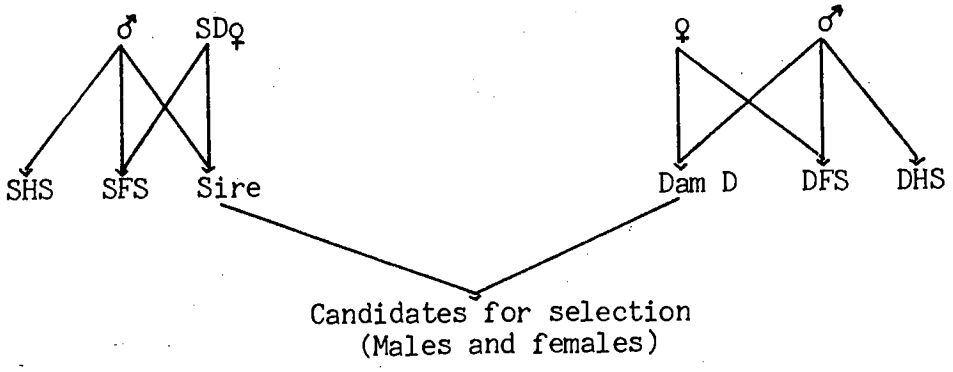
selected on two litter records of the dam and of other relatives. As a standard, the proportion selected will be 1/3 in females, and 1/d in males, selecting only one male per full sibship. Selection of whole litters of males is considered later. A mating ratio of 1 male for 10 females has been chosen as practical with natural service, but ratios of 1/5 and 1/15 are also considered.

With 10 dams per sire, candidates for selection will have information (2 litter records) on their dam (D), 2 dam's full-sibs (DFS) and 27 dam's half-sibs (DHS), and for the sire's family on 3 ? sire's full-sibs (SFS), 27 sire's half-sibs (SHS) and on the sire's dam (SD). The pedigree, structure and information, with numbers and symbols, is shown in Figure 3.1. This shows that there is much information available on relatives to assist in selection.

In order to have two litter records on all the pedigree, all females born from first litters would need to be retained and allowed to farrow twice. So, space provisions (farrowing pens) would need to be three times those normally required for breeding replacements in a nucleus herd. This requirement might be met by transferring surplus breeding females to multiplier or commercial herds and ensuring that records are kept and made available on their farrowing performance. In this way information on the full pedigree (Figure 3.1) would be available for selection at nucleus level (Case 1). If this was not possible and only selected breeding females could be retained, the numbers of full- and half-sibs would be on average one third of those given earlier (Case 2).

FIGURE 3.1

Pedigree diagram showing the information used in the family selection index, and table of the number of relatives (nd) contributing information for selection of candidates. Two litter records are available for each relative (m=2).



Family	Relative	Symbol	Number of relatives					
			Case 1			Case 2		
			All females recorded			Selected females recorded		
			n	d	nd	n	d	nd
Dam family	Dam	D	1	1	1	1	1	1
	Dam full-sibs	DFS	2	1	2	1	1	1
	Dam half-sibs	DHS	3	9	27	1	9	9
Sire family	Sire full-sibs	SFS	3	1	3	1	1	1
	Sire half-sibs	SHS	3	9	27	1	9	9
	Sire's dam	SD	1	1	1	1	1	1

III.2.1 Size of selection herd

The size of the selection herd will depend on the rate of inbreeding considered acceptable. Smith, Jordan, Steane and Sweeney (1978) found that rates of about 0.0025 per year were characteristic of several national pig breeding populations, and this has been taken as the tolerable rate of inbreeding for a selection nucleus herd. A summary of the effects of the level of inbreeding on litter size and productivity is given in Table 3.1.

TABLE 3.1

Effects of a 10% increase in inbreeding on litter size (From Hill and Webb, 1982).

Inbred genotype	Litter size	
	Born alive	56 days
Litter	-0.13	-0.34
Dam	-0.23	-0.23

The approximate equilibrium rate of inbreeding per year is (from Hill, 1972).

$$F = (1/L^2)[\ 1/8s + 1/8sd\ ]$$

where s sires and sd dams enter the breeding herd per year, and L is the generation interval, i.e. the average age of parents when their progeny are born. With L=1 and d=10, the number of sires required for $F = 0.0025$ is 55. Thus a selected herd of 55 males and 550

females would be required, with a further 1100 unselected female relatives also recorded for their litters.

The numbers could be almost halved by practicing within sire selection for males, so that each sire leaves one son (e.g. Hill, 1972). This is because most of the inbreeding is due to the lower number of sires and balancing their contribution would minimise the variation in this path. However, there would be some loss in selection response due to the within sire selection. A review of the numbers required for breeding and the selection intensities with different mating ratios for selection over sire families and within sire families is given in Table 3.2.

III.3 Selection index

The selection objective in this section is litter size. For simplicity it is assumed that the genetic correlations for litter size at different parities is one. Then the aggregate breeding value is simply:

$$H=A$$

where A is the additive genetic value for litter size with unit economic weight. A simple phenotypic model is considered first, with the phenotypic value (P) made up of the additive genetic value (A) and residual effect (R). Thus

$$P = A + R \qquad \ldots (3.1)$$

$$VP = VA + VR$$

where VP, VA and VR are the phenotypic, additive and residual variances respectively. Some of the simplifications made here are relaxed later.

TABLE 3.2

Numbers and selection intensities for an inbreeding rate of 0.0025 per year for selection of males 1) across sires 2) within sires.

	Selection of males					
	Across sires			Within sires		
Number of males used	55			30		
Mating ratio (males/females)	1/5	1/10	1/15	1/5	1/10	1/15
Number of females	275	550	825	150	300	450
Proportion selected						
Males : 1 male per litter	1/5	1/10	1/15	1/5	1/10	1/15
3 males per litter	1/15	1/30	1/45	-	-	-
Females	1/3	1/3	1/3	1/3	1/3	1/3
Standardised selection differentials						
Males : 1 male per litter	1.40	1.76	1.94	1.16+	1.54+	1.79+
3 males per litter	1.94	2.23	2.38	-	-	-
Females	1.10	1.10	1.10	1.10	1.10	1.10

+ Selection from groups of limited size

A series of selection indices are now considered, involving successively the dam, the dam family and the sire family, with 2 litter records available on all females recorded. All records are expressed as deviations from the population. The variables in the index are:

$\overline{D}$ - dam (average of two records)

$\overline{DFS}$ - dam's full-sib family mean (excluding her own records)

$\overline{DHS}$ - dam's half-sib family mean (excluding her full-sibs and own records)

$\overline{SFS}$ - sire's full-sib family mean

$\overline{SHS}$ - sire's half-sib family mean (excluding his full-sibs)

$\overline{SD}$ - sire's dam (average of two records

The first index (called the basic index) is simply based on the dam (D) of the candidates for selection (Figure 3.1).

$$I_1 = b_{11}\overline{D}$$

The second index adds information on the dam's full-sibs (DFS).

$$I_2 = b_{21}\overline{D} + b_{22}\,\overline{DFS}$$

The third index adds information on the dam's half-sibs (DHS).

$$I_3 = b_{31}\overline{D} + b_{32}\overline{DFS} + b_{33}\overline{DHS}$$

The next three indices add further information on the sire's family; in turn the sire's full-sibs (SFS), the sire's half-sib (SHS) and the sire's dam (SD).

$$I_4 = b_{41}\overline{D} + b_{42}\overline{DFS} + b_{43}\overline{DHS} + b_{44}\overline{SFS}$$

$$I_5 = b_{51}\overline{D} + b_{52}\overline{DFS} + b_{53}\overline{DHS} + b_{54}\overline{SFS} + b_{55}\overline{SHS}$$

$$I_6 = b_{61}\overline{D} + b_{62}\overline{DFS} + b_{63}\overline{DHS} + b_{64}\overline{SFS} + b_{65}\overline{SHS} + b_{66}\overline{SD}$$

This index (I_6) will be refered to as the full index because it contains the maximum information considered for selection.

Finally two other reduced indices omitting the dam's full-sibs, which may have similar maternal effects, are considered.

$$I_7 = b_{71}\overline{D} + b_{72}\overline{DHS} + b_{73}\overline{SHS}$$

$$I_8 = b_{81}\overline{D} + b_{82}\overline{DHS} + b_{83}\overline{SFS} + b_{84}\overline{SHS}$$

III.3.1 Index derivation

The index weights (**b**) are derived by solving the equation

$$\mathbf{Pb} = \mathbf{G}$$

where **P** is the phenotype matrix for the recorded variates and **G** is their covariance with the aggregate breeding value, H. The variance of H is $VH = VA = h^2VP$, where h^2 is the heritability for litter size and VP, the phenotypic variance.

The index is made up of two blocks. One is for the dam's family information and the other for the sire's. Because they are assumed independent the two parts can be derived separately.

It is convenient to give the **P** and **G** matrices for the full index (I_6) since the other cases (1-5, 7 and 8) are successive reductions from this. The general form of the full phenotypic variance covariance matrix is:

$$\mathbf{P}=VP \begin{bmatrix} \bar{D} & \overline{DFS} & \overline{DHS} & \overline{SFS} & \overline{SHS} & \overline{SD} \\ Q_{11} & t_{fs} & t_{hs} & 0 & 0 & 0 \\ & Q_{22} & t_{hs} & 0 & 0 & 0 \\ & & Q_{33} & 0 & 0 & 0 \\ & & & Q_{44} & t_{hs} & t_{dD} \\ & & & & Q_{55} & 0 \\ & & & & & Q_{66} \end{bmatrix}$$

The off-diagonal elements are expressed as intraclass correlations (t). Under the simplified assumptions of the model (3.1), these are:

t_{fs} = (VA/2)VP (from full-sib covariance)

t_{hs} = (VA/4)VP (from half-sib covariance)

t_{dD} = (VA/2)VP (from daughter-dam covariance)

The diagonal terms in **P** are of the form

$$Q_{ii} = [1 + (m-1)t + m(n-1)t_{fs} + mn(d-1)t_{hs}]/mnd \quad \ldots (3.2)$$

This formula is obtained by collecting terms of all the covariances given the family structure specified for the population. These are then expressed in terms of intraclass correlations; among m=2 individual measurements (t), among n full-sibs (t_{fs}) and among d half-sibs (t_{hs}). By substituting the relevant values for m, n and d, given in Figure 3.1 for each group of relatives, the terms for Q_{ii} can be obtained.

The genetic relationships (r) between the candidates for selection and their various relatives are given in Table 3.3. Thus

$$\mathbf{G} = \mathbf{r}VA$$

where $\mathbf{r} = (1/2, 1/4, 1/8, 1/4, 1/8, 1/4)$

TABLE 3.3

Coefficients of relationship (r) among the groups contributing information to the index and with the candidates for selection

Parent			Relationship (r)	
			With the parent	With the candidate
Dam	Dam	D	1	1/2
	Full-sibs	DFS	1/2	1/4
	Half-sibs	DHS	1/4	1/8
Sire	Full-sibs	SFS	1/2	1/4
	Half-sibs	SHS	1/4	1/8
	Dam	SD	1/2	1/4

The value of the indices may be considered in different (but equivalent) forms. One form is the correlation (r_{HI}) of the index (I) with the selected individual's breeding value (H). This is a measure of the accuracy of the index in selecting for H. The expected genetic superiority (S_H) of selected individuals (with, i, the standardised selection differential) is then,

$$\begin{aligned} S_H &= i\, r_{HI}\, \sigma_H \\ &= i\, Cov_{HI}/\sigma_I \\ &= i\, \mathbf{b}'\mathbf{G}/\sigma_I = i\, \mathbf{b}'\mathbf{P}\mathbf{b}/\sigma_I = i\sigma_I \end{aligned}$$

The estimated annual rate of genetic response at equilibrium is given by

$$r_{HI}\sigma_H(i_m + i_f)/(L_m+L_f) \qquad \ldots (3.3)$$

where L_m and L_f are the average ages of males and females when their progeny are born.

The relative contribution of any source of information to the accuracy of selection, or to the genetic response, can be measured as the proportional loss in accuracy incurred by leaving it out of the index. If the index omitting a source of information was I*, the proportional loss would be

$$(r_{HI} - r_{HI*})/r_{HI} \qquad \ldots (3.4)$$

III.4 Accuracy of selection

The results from the index calculations are given in Tables 3.4 for a heritability of litter size of 0.1, repeatability 0.15. The correlation (r_{HI}) of the average of the dam's two records, the basic index I_1, with the breeding value of candidates for selection is 0.209. The accuracy (r_{HI}) is increased steadily by successive additions of further family information to the index.

When all females are recorded (Case 1), the dam's full-sibs and half-sibs each add a 15 percent to the accuracy of the basic index. Bringing in information on the sire's family adds a further 23 percent for full-sibs and 15 percent for half-sibs . Finally with the sire's dam (using records subsequent to the selection of her son) a further small increase (5 percent) is obtained bringing the accuracy of selection of the full index I_6 up to 0.362 which gives a total of 74 percent improvement over the basic index (I_1). Two alternative combinations of the family information are given by indices I_7 and I_8.

Where only selected females are recorded (Case 2), the gains in accuracy are lower. For example with the full index, the accuracy falls from 0.362 to 0.312, a loss of 14 percent. It thus seems worthwhile to record all females born in the nucleus herd and to use the information in selection.

Similar results are presented, for the accuracy of selection with the different indices, for different values of heritability, in Table 3.5. As expected these show that if the true heritability were lower than 0.10, the gains from use of family information are even higher. Thus for a heritability of 0.05, the gains in accuracy over the basic index would rise to almost 100 percent with the full index I_6. For higher heritabilities the gains in accuracy are less, but even at a heritability of 0.15, the gains are close to 60 percent.

The contribution of each item of information to the full index (I_6) can be estimated by omitting it from the index and calculating the percentage loss in accuracy incurred. Results are presented in Table 3.6 for three levels of heritability and with all

females (Case 1) and selected females (Case 2) recorded. The records on the dam make the largest contribution, but this decreases as the heritability decreases. The half-sibs, both paternal and maternal make useful contributions, and increasingly so at low heritabilities.

TABLE 3.4

Accuracy of selection (r_{HI}) on the basic index (I_1) and relative accuracies with each added source of information. Case 1 : Records on all females, Case 2 : Records only on selected females (1/3 of all females). Heritability 0.10, repeatability 0.15

Accuracy of selection on basic index I_1 (r_{HI})	0.209	
Relative accuracy of indices	Case 1	Case 2
I_1 (D) [basic index]	100	100
I_2 (D + DFS)	115	108
I_3 (D + DFS + DHS)	131	119
I_4 (D + DFS + DHS + SFS)	154	129
I_5 (D + DFS + DHS + SFS + SHS)	169	142
I_6 (D + DFS + DHS + SFS + SHS + SD)	174	150
I_7 (D + DHS + SHS)	151	131
I_8 (D + DHS + SFS + SHS)	163	138

TABLE 3.5

Accuracy of selection (r_{HI}) on the basic index (I_1) and the relative accuracies with each added source of information. Repeatability 0.15

Heritability	0.05		0.10		0.15	
Accuracy of selection on the basic index I_1 (r_{HI})	0.147		0.209		0.255	
Case	1	2	1	2	1	2
Indices	Relative accuracies					
I_1(D) [basic index]	100	100	100	100	100	100
I_2(D + DFS)	119	110	115	108	112	107
I_3(D + DFS + DHS)	147	126	131	119	121	114
I_4(D + DFS + DHS + SFS)	169	136	154	129	144	125
I_5(D + DFS + DHS + SFS + SHS)	192	151	169	142	154	136
I_6(D + DFS + DHS + SFS + SHS + SD)	198	159	174	150	159	143
I_7(D + DHS + SHS)	172	137	151	131	139	126
I_8(D + DHS + SFS + SHS)	185	145	163	138	150	132

Cases 1 & 2, see Table 3.4

TABLE 3.6

Percent loss in accuracy of selection from omitting each source of information in turn from the full index (I_6), for different values of heritability. Repeatability 0.15.

Heritability		0.05		0.10		0.15	
Case		1	2	1	2	1	2
Source omitted		Percent loss in accuracy					
Dam family records							
Dam	D	11	20	12	20	14	21
Dam's full-sibs	DFS	4	4	3	3	3	2
Dam's half-sibs	DHS	10	8	7	6	5	4
Sire family records							
Sire's full-sibs	SFS	6	4	5	3	4	3
Sire's half-sibs	SHS	11	9	9	8	7	8
Sire's dam	SD	3	5	3	5	3	5

Cases 1 and 2, see Table 3.4.

III.5 Selection responses

The estimated genetic responses to selection can now be derived. A reference set of parameters, the most plausible for selection in a nucleus herd for litter size, is given in Table 3.7. They are also used later for comparing different selection systems. In the nucleus herd, selection of female candidates is limited by the litter size and survival in first parities. The proportion selected is set at 1 in 3, so the standardised selection differential is 1.10. Three options are considered for selection of males. The first and reference option is to select on the full index (I_6) but selecting only one male from each litter, so that the proportion selected is 1/d, or 1 in 10 in the reference case. However there will be an average 3 males per litter, and all might be used. This second option uses only the highest ranking candidate full sibships, giving a proportion 1/3d of males selected. However the rate of inbreeding will be higher with this system since groups of full-sib males will be used. The third option is to practice within sire selection of males, so that each sire leaves a son. This would allow the size of the nucleus herd to be reduced (as shown earlier) at the same level of inbreeding. In this case the selection differentials are adjusted to take account of the limited number (d) of dams per sire.

The estimated annual genetic response to selection using eq. 3.3 and the reference set of parameters (Table 3.7) is,

$$0.362 \cdot \sigma_A \cdot (1.76 + 1.10)/(1+1)$$

$$= 0.52\ \sigma_A \text{ per year}$$

$$= 0.46 \text{ pigs per year}$$

TABLE 3.7

Reference set of parameters used, for comparison of different selection methods.

Mean litter size		10.0
Phenotypic variance	VP	8.1
Heritability	h^2	0.1
Additive genetic variance	VA	0.81
Repeatability	t	0.15
Correlation among full sibs ($h^2/2$)	t_{fs}	0.05
Correlation among half sibs ($h^2/4$)	t_{hs}	0.025
Generation interval : males	L_m	1
females	L_f	1
Mating ratio	s/d	1/10
Proportion selected : males	s/d	1/10
females	1/3	1/3
Standardised selection differential		
males	i_m	1.76
females	i_f	1.10

With an average of 10 pigs born per litter, this represents an annual rate of improvement of 4.6 percent of the mean per year. If only selected females are recorded (Case 2), the rate of response would be about 4.0 percent (14 percent less).

The accuracy of selection and rates of response for other mating ratios and heritabilities are given in Table 3.8. With

higher mating ratios there will be more half-sibs recorded, so selection accuracy is improved. The selection differentials for males (here one male per litter) are also higher, so the rates of response are further improved. Of course with higher heritabilities the rates of response are higher for example 0.52 vs 0.58 σ_A units per year, or 0.46 vs 0.64 pigs per year for heritabilities of 0.1 and 0.15 respectively.

TABLE 3.8

Accuracy of selection on the full index I_6 and rates of genetic response for different heritabilities and mating ratios. One male per litter selected

Heritability		0.05		0.10		0.15	
Case		1	2	1	2	1	2
Mating ratio		Accuracy (r_{HI})					
1/5		0.26	0.21	0.34	0.29	0.39	0.35
1/10		0.29	0.23	0.36	0.31	0.41	0.37
1/15		0.31	0.25	0.37	0.33	0.42	0.38
	i^+	Genetic response in σ_A units/year					
1/5	1.40	0.33	0.27	0.42	0.36	0.49	0.43
1/10	1.76	0.41	0.33	0.52	0.44	0.58	0.52
1/15	1.94	0.47	0.38	0.57	0.49	0.63	0.57

Cases 1 and 2, see Table 3.4
+ standardised selection differential

The rates of response will also be higher if all males in a litter are used for breeding, as shown in Table 3.9. For the reference case the response rises from 0.52 to 0.60 σ_A, a gain of 15 percent.

TABLE 3.9

Rates of genetic response from selection on the full index I_6 for different heritabilities and proportions selected (p). All males used from top ranking candidate litters.

Heritability			0.05		0.10		0.15	
Case			1	2	1	2	1	2
Mating ratio	p	i^+	Genetic response in σ_A units/year					
1/5	1/15	1.94	0.39	0.32	0.52	0.44	0.59	0.53
1/10	1/30	2.23	0.48	0.39	0.60	0.52	0.68	0.61
1/15	1/45	2.38	0.53	0.43	0.65	0.57	0.72	0.65

Case 1 and 2 : see Table 3.4
+ standardised selection differential

The possibility of reducing the size of the nucleus herd at the same rate of inbreeding was considered, using within sire selection of males. As discussed earlier, the sire family information is common to all males in the sire family, so index I_3 using only the dam family is then appropriate for selection of males. Other adjustments must be made to the standardised selection differential of males selected from a small group of litters. For the reference case, the estimated response becomes:

$$[0.273(1.54) + 0.363(1.1)]/(1+1)$$

$$= 0.41\ \sigma_A \text{ per year}$$

The loss in response, compared with the reference case ($0.52\sigma_A$) is over 20 percent. Comparative responses for other mating ratios and heritabilities are given in Table 3.10.

The rates of response for the three modes of selection of males are summarised for the reference parameters in Table 3.11.

TABLE 3.10

Accuracy of selection on index I_3, using dam family information and rates of genetic response from selection of males within sire family (using I_3) and selection of females across sire families (using I_6)

Heritability		0.05		0.10		0.15	
Case		1	2	1	2	1	2
Mating ratio		Accuracy (r_{HI})					
1/5		0.20	0.17	0.26	0.24	0.30	0.28
1/10		0.22	0.19	0.27	0.25	0.31	0.29
1/15		0.23	0.19	0.28	0.26	0.32	0.30
	i^+ (males)	Genetic response in σ_A units/year					
1/5	1.16	0.26	0.21	0.34	0.30	0.39	0.35
1/10	1.54	0.33	0.27	0.41	0.36	0.46	0.42
1/15	1.79	0.37	0.31	0.45	0.41	0.51	0.48

Cases 1 and 2, see Table 3.4
+ Standardised selection differentials for small numbers (Becker, 1975)

TABLE 3.11

Comparison of rates of genetic response for three modes of selection of males. (Reference set of parameters, see Table 1.7)

Male selection	p^+	i^{++}	Case 1 Genetic response (σ_A)	Case 1 (pigs)	Case 2 (units/year) (σ_A)	Case 2 (pigs)
Within sires	1/10	1.54	0.41	0.37	0.36	0.33
Across sires						
One male/litter	1/10	1.76	0.52	0.46	0.47	0.42
Three males/litter	1/30	2.23	0.60	0.54	0.55	0.49

Cases 1 and 2, see Table 3.4
+ proportion selected
++ standardised selection differential

III.6 Discussion

These results confirm those of Ollivier (1974) in that appreciable rates of genetic response in litter size should be possible by selection. With the use of family information even higher rates are predicted. The result is surprising in that a response (for the reference case) of 4.6 percent of the mean per year might be achieved. This, in fact, exceeds the expected rates of genetic response for growth rate (2-3%) or lean percent (1-2%) (Smith, 1984). Yet these are both moderately heritable traits where selection can be on individual performance for both sexes. The high rates of response for litter size are due to the large coefficient

of variation (0.28), the availability of records on many relatives and the short generation interval (1 year). This more than compensates for the disadvantages mentioned earlier.

The use of index selection has received little attention previously in selection for litter size though Hill and Webb (1982) mention the possibility. Yet its use is standard in selection of egg laying poultry (Osborne, 1957) and more recently in dairy cattle (Hill and Swanson, 1983) and experimentally in sheep (Martin and Smith, 1980). The higher accuracy of selection with family information also increases the relative importance of litter size in a selection index containing growth, carcass and reproductive traits. This will be discussed in Chapter 7.

The selection scheme calls for a rather large herd, to maintain a low rate of inbreeding. For the reference case of 0.0025 inbreeding per year this required 55 males, 550 selected females. Another 1100 females were kept for their records with all females kept for two litters. This rate of inbreeding is considered acceptable (national average) but higher rates of inbreeding could well be tolerated, reducing the size of herd required proportionally. Within sire selection would approximately halve the rate of inbreeding, but also reduces the responses by about 20 percent. With index selection it may be that the rates of inbreeding are higher than specified (e.g. Robertson, 1961; Burrows, 1984) since related individuals would tend to be selected. This effect might be offset by selecting at a rate of 1/10, but using all (3) males in a litter, so that 55 x 3 males in total would be used. This would reduce subsequent sibship size and therefore the accuracies and response to selection somewhat. However, in

practice, information on litter size would be combined in an economic selection index for all economic traits and in that case the selection among males on index will be at a rate of 1/30 (for the reference case) since it is unlikely that more than one male per litter will be selected on the combined index.

The effect of selection on the genetic variation available for selection in the next generation (Bulmer, 1971) has been ignored since the selection is neither very intense ($\hat{h}$) or accurate. Also, it might be argued that the first two litter records of the sire's dam (SD) will have been used previously in selecting the sire and thus would be of little value in further selection. Therefore, litters 3 and 4 of SD could be used in the index for selection of grand progeny since there is such a low correlation between succesive litters. In any case, this should not be of major concern since the records of SD only contribute about 5 percent to the accuracy of the full index.

PIC data was examined to see how much family information was available in practice. Birth date and age at the end of performance testing was recorded for all breeding sows. Hence, it was simply a matter of counting all family records available at the time corresponding to the selection of candidates. It was only possible to take account of dam family records. On average there were 1.43 records on the dam (D), with 1.19 and 10.18 first parity records on full-sibs (DFS) and half-sibs (DHS) respectively. Second parity records were fewer with 0.82 and 6.19 for DFS and DHS respectively. With no special provisions these average values are very close to the expected with replacement of 1/3 of females and a

mating ratio of 1:10. The distribution of records is shown in Figures 3.2 to 3.4. These figures clearly illustrate two problems that will commonly be found in practice. One is the variation in amount of information available for particular candidates. For example, most dams will have two records, all a first parity, of course, but some will have no second parity (Figure 3.2). A much larger variation is to be expected for the number of full-sibs with a first parity record; ranging from 0 to 6 (Figure 3.3). The range is even larger for half-sib records, 0 to 33 (Figure 3.4). The second point illustrated by these figures is that the maximum information will be available from first parity records. This is because families will be spread in time so that at the time of selection all females will have had a chance to produce a first record, but a few will be awaiting their second record or will not produce one at all. Hence, indices with variable numbers are needed. In order to have continuous farrowings, sows and boars must be batched so that information for selection is available when required. Some migration of genes across groups would be needed to minimize inbreeding. Since sires and dams are considered to be unrelated, sub indices for the paternal and maternal family information can be calculated separately (for ease of computation) and then combined. Also, the index matrices can be expressed in alternate ways. By expressing observations as within family deviations they can be made diagonal and thus further simplify computations (see Sales and Hill, 1976, for example).

Finally, the standard values used might be considered too conservative. Yet, in practice there is always some attrition of the rates of genetic change possible, due to mortality, necessary

culling, infertility, errors in selection and other factors. Additionally, to offset these problems it would be desirable to maintain some 10 percent spares (and matings) by keeping a few extra males and any surplus females from selected sibships.

In the next Chapter it will be shown that the presence of maternal effects, and common environmental effects among full-sibs, may reduce those estimated changes somewhat.

FIGURE 3.2 Distribution of the number of records available on the dam of candidates for selection (PIC data).

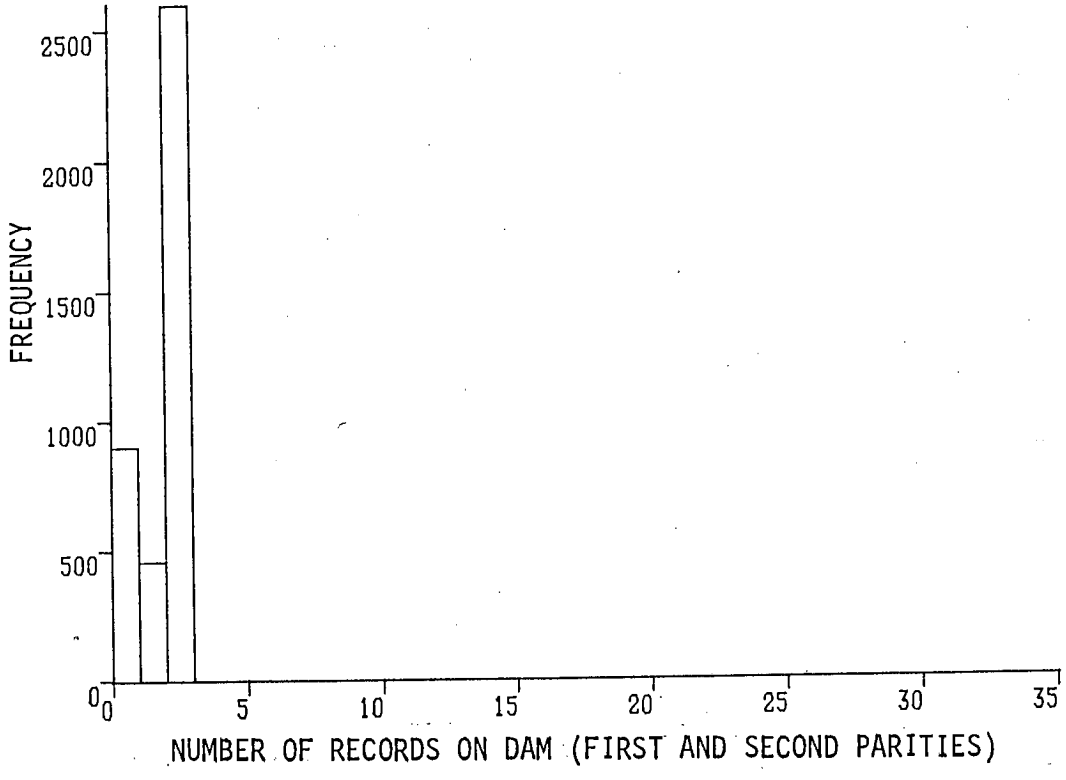
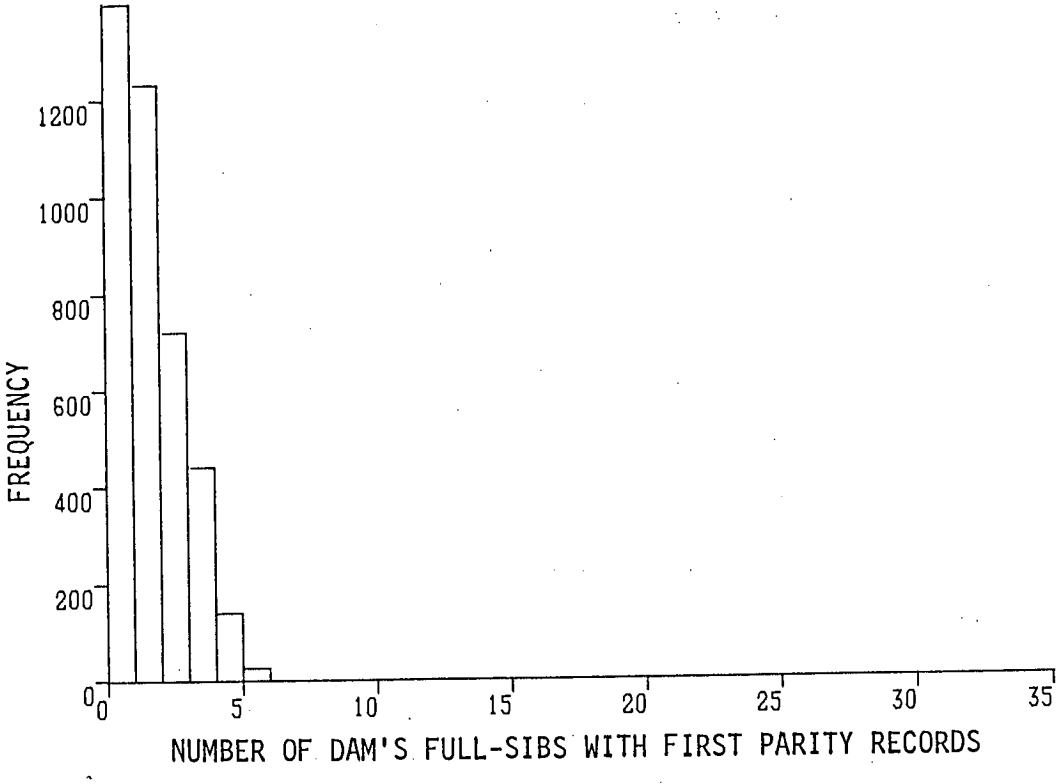


FIGURE 3.3 Distributions of the number of dam's full-sib records available for selection candidates (PIC data).



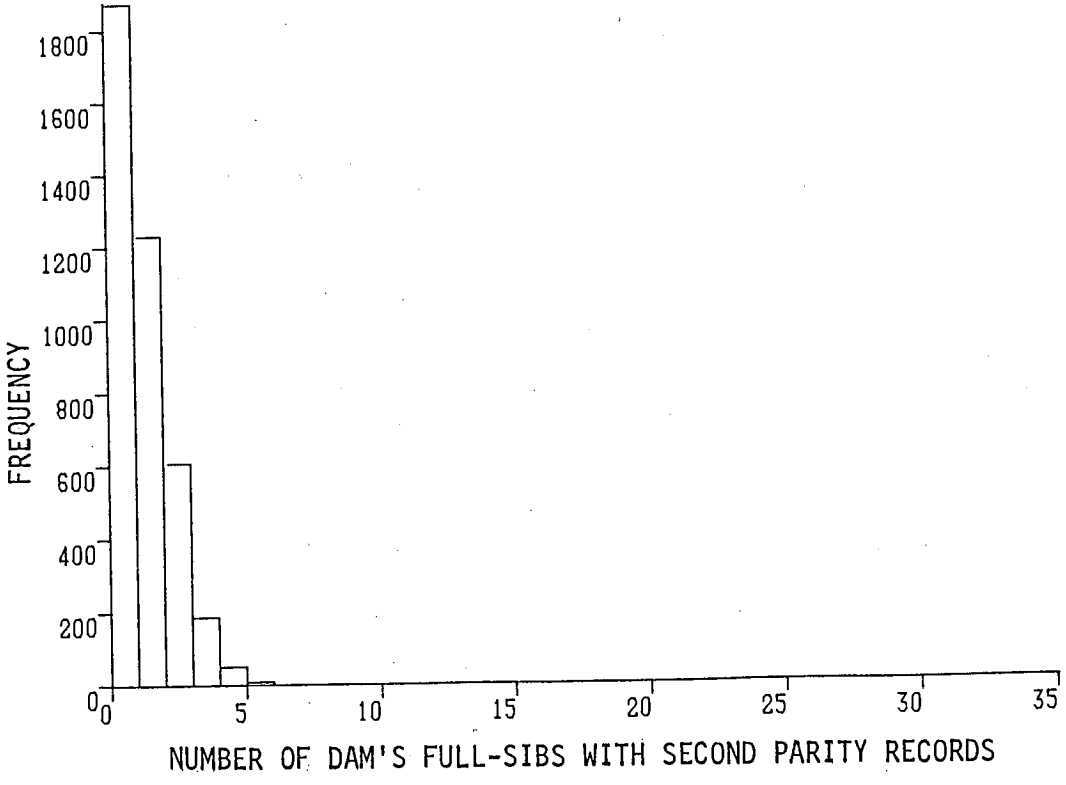
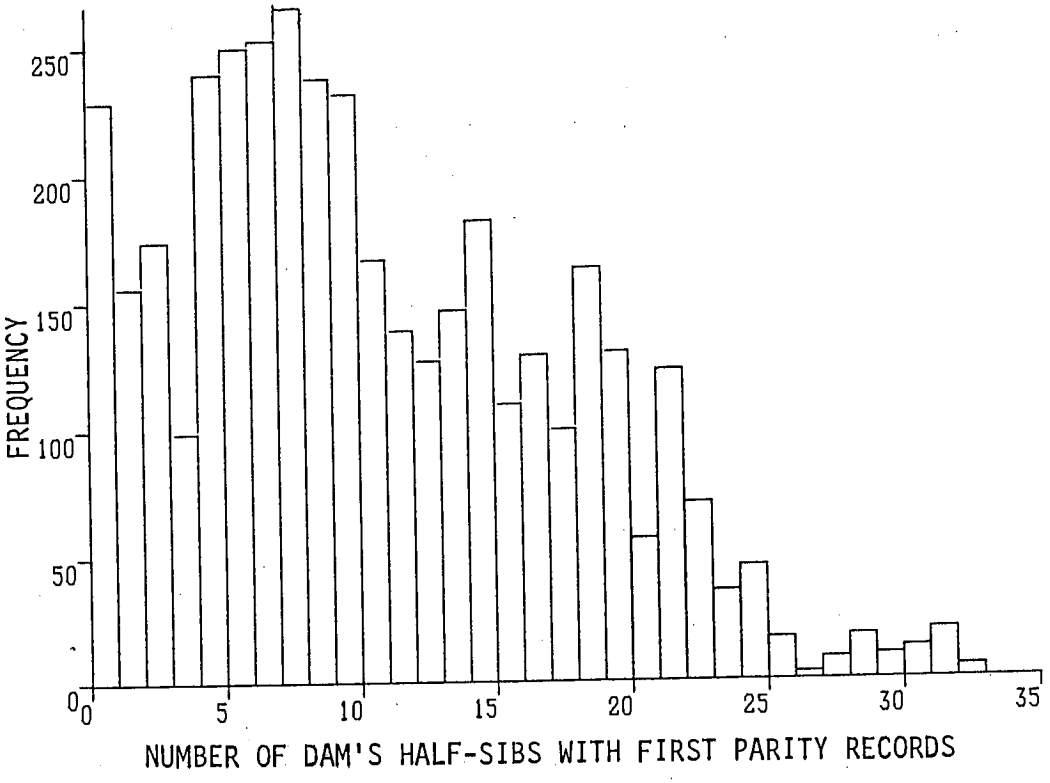
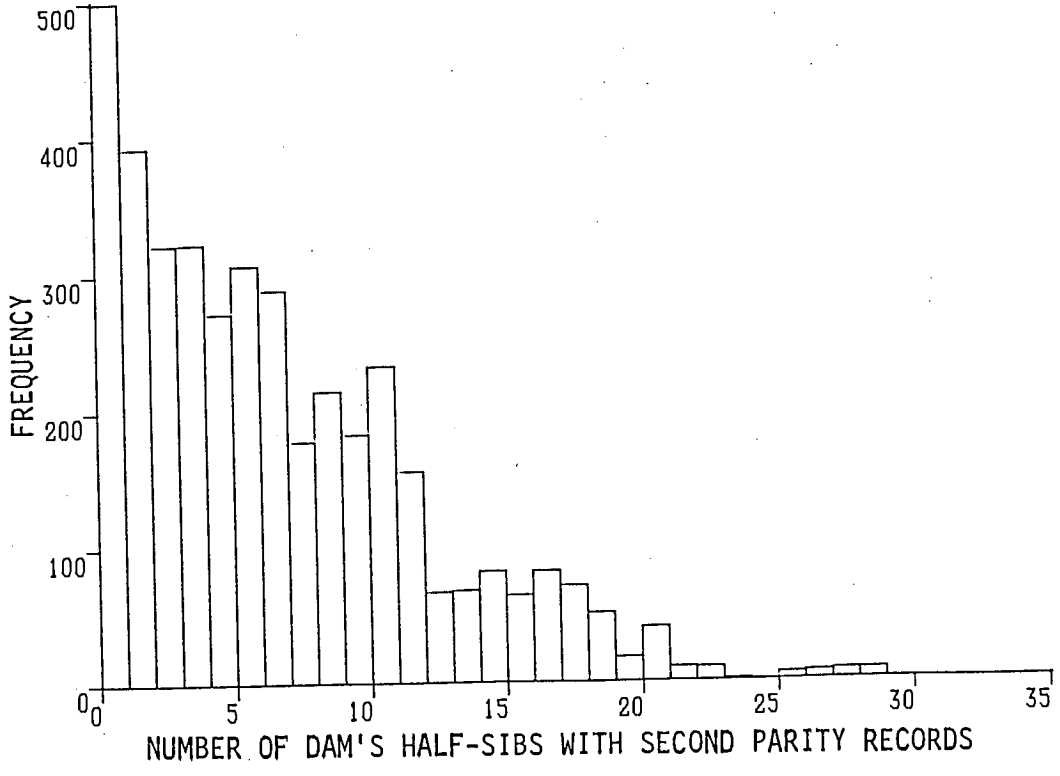


FIGURE 3.4 Distributions of the number of dam's half-sib records available for selection candidates (PIC data).





CHAPTER IV. INDEX SELECTION. Model including maternal environmental effects.

IV.1 Introduction

Index calculations in the previous Chapter were done on the simplified assumption that additive effects are the only cause of resemblance among relatives. In pigs, a dam contributes most of the prenatal environment of her progeny. In many cases she will also provide a large part of their early post natal environment. This maternal environment may affect the progeny's performance for other traits (see Robison, 1981 for a review). As a consequence of this, maternal effects are a frequent source of environmental resemblance particularly affecting the covariance of full-sibs, and the covariance of dam with offspring. The possible consequences of ignoring some of these environmental sources of variation in the previous index calculations are studied in this section.

The following simple model has been used to separate the phenotype (P) into independent components.

$$P = A + M + C + E + R$$

where:

A is an additive genetic effect

M is a function ($\hat{m}$) of the dam's phenotype (P'), with $M = \hat{m}P'$ following Falconer (1965)

C is an environmental effect common to all members of a litter and independent of M

E is a permanent environmental effect special to the individual not included in M or C

R is a temporary residual effect.

The assumptions in the model are: uncorrelated effects, unity of genetic correlation between parities, and that environmental effects (M, C and E) are permanent.

It follows from this model that all the covariances needed for the index calculations can simply be derived by defining the phenotypes. For example, the covariance of phenotype (P) with breeding value (A) would be

$$Cov_{A,P} = Cov_{A,(A+\hat{m}P')} = Cov_{A,A} + Cov_{A,\hat{m}P'}$$

since all other terms are zero by definition.

$$Cov_{A,A} = VA$$

$$Cov_{A,\hat{m}P'} = \hat{m}[Cov_{A,A'} + \hat{m}(Cov_{A,A''} + \ldots \text{ etc})]$$

where each (') indicates an additional generation back. Then

$$\begin{aligned} Cov_{A,\hat{m}P'} &= \hat{m}[VA/2 + \hat{m}(VA/4 + \ldots \text{ etc })] \\ &= VA[\hat{m}/2 + \hat{m}^2/4 + \ldots \text{ etc}] \\ &= VA[\hat{m}/(2-\hat{m})] \qquad \ldots (4.1) \end{aligned}$$

Therefore,

$$\begin{aligned} Cov_{A,P} &= VA[(1 + \hat{m}/(2-\hat{m})] \\ &= VA[(2/(2-\hat{m})] \qquad \ldots (4.2) \end{aligned}$$

IV.2 Index derivation

The index weights (**b**) are derived by solving the equation

$$\mathbf{Pb} = \mathbf{G}$$

The matrices are as before (Chapter 3) except that their elements are now derived following the less simple model. Derivation of the

covariances needed to substitute into **P** are straight forward.

Covariance of repeated records

$$Cov_{Pi,Pj} = VA + 2VA[\hat{m}/(2-\hat{m})] + \hat{m}^2VP + VC + VE$$

$$= VA\,[1 + 2\hat{m}/(2-\hat{m})] + \hat{m}^2VP + VC + VE$$

with repeatability

$$t = h^2[1 + 2\hat{m}/(2-\hat{m})] + \hat{m}^2 + c^2 + e^2$$

Covariance of full-sibs

$$Cov_{fs} = (VA/2)[1 + 2\hat{m}/(2-\hat{m})] + \hat{m}^2VP + VC$$

with intraclass correlation

$$t_{fs} = (h^2/2)[1 + 2\hat{m}/(2-\hat{m})] + \hat{m}^2 + c^2$$

Covariance of half-sibs

$$Cov_{hs} = VA/4$$

with intraclass correlation

$$t_{hs} = h^2/4$$

and the daughter-dam covariance

$$Cov_{P,P'} = (VA/2)[1 + 2\hat{m}/(2-\hat{m})] + \hat{m}VP'$$

assuming $VP' = VP$

$$t_{P,P'} = t_{d,D} = (h^2/2)[1 + 2\hat{m}/(2-\hat{m})] + \hat{m}$$

Adjustments are also needed for the vector **G**. The covariances involved are simply derived and it turns out that a correction term invoving $VA[\hat{m}/(2-\hat{m})]$ derived in (4.1) can be added to **G** according to the following formula

$$\mathbf{G} + VA[\hat{m}/(2-\hat{m})][1/2,1/2,0,1/2,0,1/8]'$$

IV.3 Index calculations

A range of values for h^2, $\hat{m}$ and c^2 in various combinations were set. Number of relatives and records were also varied. Three values of h^2 were used (0.05, 0.10 and 0.15), three for c^2(0, 0.025

and 0.05) and three values for $\hat{m}$ (0, -0.05 and -0.125). These were thought to represent the most likely parameter space. For each combination of these parameters, the optimum index (I) was computed, with accuracy (r_{HI})

$$r_{HI} = \mathbf{bG}\cdot[\mathbf{b}'\mathbf{Pb}\ \sigma_H^2]^{-1/2}$$

The simple additive model is represented when $\hat{m}^2 = c^2 = 0$ with index weights denoted b_o and accuracy r_{HIo}. Then, the accuracy of using the (wrong) index weights, b_o, for each combination of parameters was computed and denoted (r_{HI}*) when $\hat{m}^2 \neq 0$, $c^2 \neq 0$. Thus

$$r_{HI}^* = b_o\mathbf{G}\cdot[b_o'\mathbf{P}b_o\ \sigma_H^2]^{-1/2} \text{ for } \hat{m}^2 \neq 0,\ c^2 \neq 0$$

The relative efficiency resulting from using the wrong index weights has been measured as r_{HI}^*/r_{HI}. This identifies the loss in predicted progress versus achieved progress given the same aggregate genotype, but using wrong index weights (i.e. b_o). The loss in progress predicted from assuming a simple additive model versus the predicted progress under less simplified assumptions (i.e. taking account of maternal environmental effects), has been computed as r_{HI}/r_{HIo}. Finally, the combined effects of the two sources of error is given by the product of the two ratios. For convenience the three ratios have been transformed and expressed on a percent basis as (1-ratio)(100).

IV.4 Loss in selection efficiency

Table 4.1 shows the accuracies of the indices for the simple additive model (r_{HIo}, with $\hat{m} = c^2 = 0$) for different values of heritability and different amounts of family information. The

loss in efficiency from using the wrong index weights (from r_{HI}^*/r_{HI}) is near zero in most cases studied with a maximum loss of 3% (Table 4.2). The loss in progress that would be expected from models with maternal environmental effects relative to a simple additive model (from r_{HI}/r_{HIo}) is considerably larger with expected losses varying from 1 to 10% (Table 4.3). The two sources of error combined would lead up to 13% overestimation of response to selection in the more extreme cases studied, as shown in Table 4.4.

TABLE 4.1

Accuracies of indices with different amounts of family information and a range of parameter values in the absence of maternal environmental effects (using b_o).

Half-sib families d dams, n progeny/dam			9 n=3, d=10	4 n=3, d=5	0 n=3, d=1
Parameter settings+			Accuracy of index		
$\hat{m}$	c^2	h^2			
0	0	0.05	0.30	0.27	0.23
0	0	0.10	0.36	0.34	0.30
0	0	0.15	0.40	0.39	0.35

+ $e^2 = 0.05$

TABLE 4.2

Overestimation[+] of response to index selection from true parameter values for maternal environmental effects (using wrong index weights b_o).

Half-sib families in I		9			4			0		
d dams, n progeny/dam		n=3, d=10			n=3, d=5			n=3, d=1		
Heritability		0.05	0.10	0.15	0.05	0.10	0.15	0.05	0.10	0.15
Parameter settings[++]		Percent loss in expected progress								
c^2	$\hat{m}$									
0	-0.050	0	0	0	0	0	0	0	0	0
0	-0.125	1	1	1	2	1	1	3	2	2
0.025	0	0	0	0	0	0	0	0	0	0
0.025	-0.050	0	0	0	0	0	0	1	0	0
0.025	-0.125	1	1	1	2	1	1	3	2	2
0.050	0	0	0	0	0	0	0	0	0	0
0.050	-0.050	0	0	0	1	0	0	1	1	1
0.050	-0.125	1	1	1	2	2	1	3	3	2

[+] $100(1 - r_{HI}^*/r_{HI})$

[++] $e^2 = 0.05$

TABLE 4.3

Overestimation[+] of response to index selection in the presence of maternal environmental effects, relative to the predicted response from a simple additive model.

Half-sib families	9			4			0		
d dams, n progeny/dam	n=3, d=10			n=3, d=5			n=3, d=1		
Heritability	0.05	0.10	0.15	0.05	0.10	0.15	0.05	0.10	0.15
Parameter settings[++]	Percent loss in expected progress								
c^2 $\hat{m}$									
0 -0.050	1	1	1	1	1	1	1	1	1
0 -0.125	2	2	2	2	3	3	3	3	3
0.025 0	3	2	2	4	3	2	4	3	3
0.025 -0.050	4	3	3	4	4	3	5	5	4
0.025 -0.125	5	5	4	6	5	5	7	6	6
0.050 0	6	5	4	7	5	5	7	6	6
0.050 -0.050	7	5	5	8	6	6	8	8	7
0.050 -0.125	8	7	6	9	8	7	10	9	9

[+] $100(1 - r_{HI} / r_{HIo})$

[++] $e^2 = 0.05$

TABLE 4.4

Overestimation of response to index selection combining the two sources of error in Tables 4.2 and 4.3.

Half-sib families in I		9			4			0		
d dams, n progeny/dam		n=3, d=10			n=3, d=5			n=3, d=1		
Heritability		0.05	0.10	0.15	0.05	0.10	0.15	0.05	0.10	0.15
Parameter settings+		Percent loss in expected progress								
c^2	$\hat{m}$									
0	-0.050	1	1	1	1	1	1	1	2	2
0	-0.125	3	3	3	4	4	4	5	5	5
0.025	0	3	2	2	4	3	3	4	4	3
0.025	-0.050	4	3	3	5	4	4	6	5	5
0.025	-0.125	6	6	5	8	7	6	9	9	8
0.050	0	6	5	4	7	6	5	8	7	6
0.050	-0.050	7	6	5	8	7	6	9	8	8
0.050	-0.125	9	8	7	11	9	9	13	12	11

+ $e^2 = 0.05$

IV.5 Discussion

Two sources of error which could affect the predicted responses from index selection were treated separately. The first, identifies the loss in efficiency from using the wrong index weights relative to the optimum solution given the true parameters (r_{HI}^*/r_{HI}). This sets the problem in a similar framework as Sales and Hill (1976) and as expected there is little loss in efficiency. This says that the ranking of selected individuals is little affected by wrong parameter estimates. Most of the loss comes from the effects of $\hat{m}$ rather than c^2 despite smaller absolute values of the former. This probably reflects the relative importance of the

dam's record in the index and the effect of $\hat{m}$ (and not c^2) on this covariance.

The second source of error identifies the loss in predicted response to index selection resulting from the effects of $c^2 \neq 0$ and $\hat{m} \neq 0$ relative to predictions from a simple additive case (r_{HI}/r_{HIo}). This refers to the slopes of the expected responses under different models and has a much larger effect. The product of the two gives the best estimate of the relative amount by which response to selection could be overestimated from assuming a simple additive model versus the achieved progress in the presence of real maternal environmental effects of the sort discussed.

The problem of overestimating the response to selection for litter size on dam's records was studied empirically by Van der Steen (1983). He concluded that a loss in response between 5% and 11% could be expected for values of $\hat{m}$ lying between -0.1 and -0.2. It can be shown theoretically (from eq. 4.2) that the proportional efficiency of selection on the dam's record alone is $2/(2-\hat{m})$, or 0.95 for $\hat{m}$=-0.1, the literature average estimate, and does not depend on the heritability of the trait. Thus, the use of the full index aproximately halves this potential loss. If parameter values for $\hat{m}$ are known with confidence, records can be adjusted statistically. Alternatively, equalizing of litters at birth would get rid of most of this effect. However, it would be difficult to adjust records for common litter environmental effects (c^2) since they are unique to the individual litter. Also, there are few parameter estimates for $\hat{m}$ and c^2 in the literature and these are in any case difficult to estimate. Hence, it was important to study the

possible consequences on previous calculations of ignoring such effects.

It is difficult to decide a priori on some upper limit for the value of c^2 to be used and 0.05 is possibly high. However, variance due to dominance has also been ignored. Effects due to dominance are expected for a trait showing heterosis and together with c^2 specially affect the covariance of full-sibs. Considered jointly, they could inflate considerably this covariance. Hence although a value of $c^2 = 0.05$ might be believed too high, the effect on the index of a correspondingly large value for t_{fs} is worth considering. The sensitivity of the index predictions ignoring $c^2 \neq 0$ is a good reminder of the large contribution made by full-sib family means to the index.

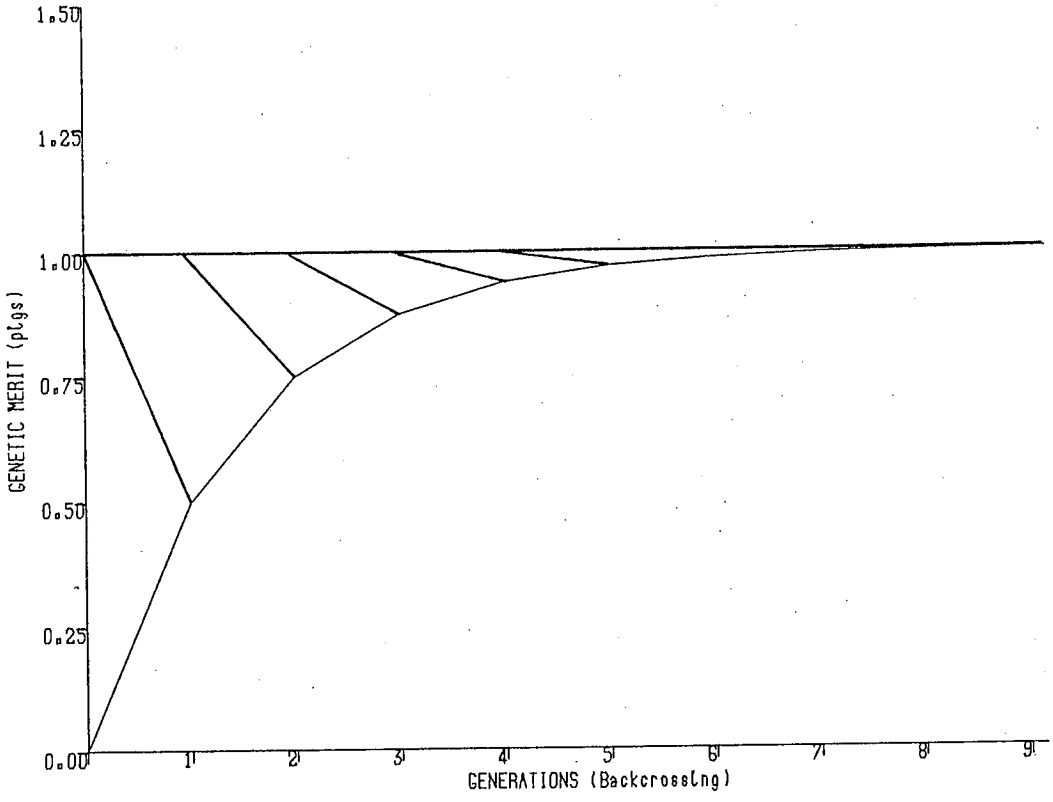
CHAPTER V. HYPERPROLIFIC SELECTION

V.1 Introduction

So far the selection schemes considered are based on individuals from closed nucleus herds. Recently, Legault and Gruand (1976) proposed extending the selection for litter size to a broader base by selecting intensively from a large 'national' population of litter recorded females. Very large selection differentials could then be achieved by selecting the most extreme individuals. They used the terms 'hyperprolific sows' and 'hyperprolific lines' to describe such groups and these terms are now widely used.

The main feature of a hyperprolific selection scheme is that a broad base (B) population of sows is continuously screened and sows with extreme litter sizes, on one or several records, are selected. At discrete intervals (say each year) the top 1 or 2 percent of sows are selected. The first lot of selected sows is backcrossed to each others sons (from average males). Thereafter, each subsequent batch of selected sows is backrossed to the males from the previous batch. The genetic difference between selected dams and their progeny is thus halved each generation as shown in Figure 5.1. If selected sows have a genetic merit Δ, above the contemporary mean, the expected genetic merit of the successive progeny groups would be $1\Delta/2$, $3\Delta/4$, $7\Delta/8$, ... etc. A target of $7\Delta/8$ might be set and a cycle considered complete when progeny of selected sows reached this level.

FIGURE 5.3 Genetic merit of progeny from 'hyperprolific' sows following several generations of backcrossing. 'Hyperprolific' sows selected with genetic merit of 1 pig 1_{Δ} (from Legault and Gruand, 1976).



In their original proposal, Legault and Gruand (1976) considered using males produced in this way for improvement of the national herd through artificial insemination (AI). They considered the theoretical consequences of a single cycle of selection. However, their scheme could be used repeatedly. So in the first part of this Chapter, the hyperprolific scheme is extended to consider the annual rate of improvement in litter size from successive cycles of selection (continuous hyperprolific scheme).

Some pig breeding companies have already adopted the basic ideas of the scheme for a somewhat different purpose, namely the creation of specialised dam lines. Some of the features of this approach are discussed in a later section, 'Hyperprolific dam lines'.

V.2 Continuous hyperprolific scheme

The main objective of the system is to select sows with very large litters from a broad base population (B) and to disseminate their genes through the population by means of AI from their sons. The selection system was described earlier and is now shown in Figure 5.2 together with the schedule of events described in Table 5.1. The population of sows is continuously screened and the top 1 or 2 percent selected. Here selection will be on the average of two litter records, as the reference case. The selected sows are introduced into the hyperprolific nucleus herd (H) and used to produce sons which are then used simultaneously both in the nucleus and in the population by AI.

TABLE 5.1

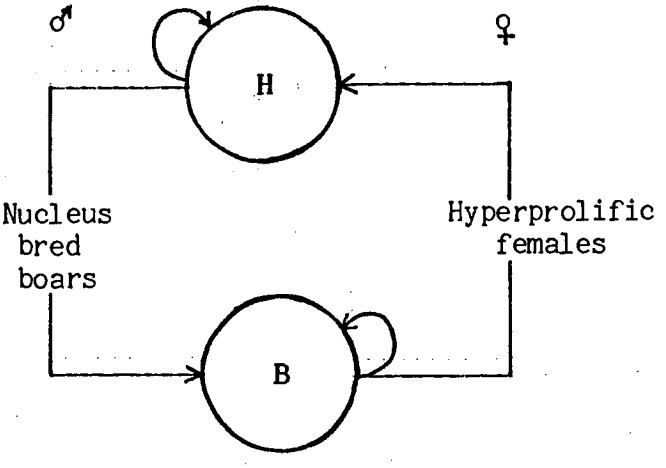
Diagram and schedule of events in a continuous 'hyperprolific scheme'

Gene flow	Events	Time period Months(y)+	Comments
→Base population	Birth	0(1)	
(B)	Mating	6(2)	
	1st Parity	12(3)	
	2nd Parity	18(4)	Select top 2% sows, introduce in nucleus
→Selected sows and progeny	Mating	24(5)	
(H)	Progeny born	30(6)	
	Male progeny available for breeding	36(7)	To be used through AI on base population

+ Age class

FIGURE 5.2

Gene flow diagram for continuous 'hyperprolific scheme'. Case 1.



H - Hyperprolific Nucleus
B - Base population

Evaluation of the annual genetic response is best done by tracing the dissemination (transfer) of genes in time through a system specified by the age structure of the breeding population. This 'gene flow technique' is based on the methods of Hill (1974) using a general transition probability matrix, applied to animal breeding problems. The methods are given in Hill (1974) so only the relevant matrices and assumptions are described here.

Three possibilities are considered. In the first (1) all the base population sows (B) are artificially inseminated to the same boars that are used in the nucleus hyperprolific herd (H). This possibility resembles the original scheme of Legault and Gruand (1976), but the scheme is extended to several cycles of continuous selection. The second and third possibilities (2 and 3) assume that only one third or one sixth, respectively, of the sow replacements in B are progeny of boars from the hyperprolific nucleus. The rest are progeny of other commercial boars (C). These boars may be selected or unselected for other traits and are assumed average for litter size. If the commercial boars were used only as terminal sires, with all progeny slaughtered, then case 1 would apply. There are, of course, many intermediate situations possible and alternative population structures. The intention here is to study two extreme and one intermediate case to illustrate some practical consequences of applying such a scheme continuously on a national basis.

V.2.1 Gene flow

The system can be specified simply by the passage of genes through four paths. These are H males to produce progeny in H, B females to produce progeny in H, H males to produce progeny in B and B females to produce progeny in B. These four paths constitute the blocks in the **P** matrix which specifies the passage of genes from one path to another in the whole system. A diagram of the selection system together with the relevant (condensed) matrices used for the analysis are shown in Table 5.2 for case 1 (cases 2 and 3 are summarised in the Appendix A5.1).

V.2.2 Structure of **P** matrix

The main concern here is the passage of genes from breeding animals to progeny . Since pigs can first farrow when one year old and subsequently every 6 months, it is convenient to express their age (y) in six month time periods. Following the system and time schedule in Table 5.1 and making some additional specifications, the structure of **P** can be derived. It is worthwhile stressing at this point that the matrix **P** is essential to the analysis since it specifies both the initial stages of the process and the final equilibrium. Consider that progeny in H get half their genes from males themselves born in H one time period earlier (one year olds). The other half of their genes come from selected sows born in the base population 6 time periods earlier. That is they were selected after their second parity records at time period 4; then were introduced into H and mated at time period 5 and have their progeny six months later at the age of 3 years, time period 6.

TABLE 5.2

Relevant matrices for gene flow methods and computation of uniform rates of response to selection. Case 1.

Condensed matrices

Paths of gene flow (Blocks in P matrix)

$$\begin{bmatrix} \text{H males to H} & \text{B females to H} \\ \text{H males to B} & \text{B females to B} \end{bmatrix}$$

Age class (breeding)

$$\left[\begin{array}{cc|cccccc} 1 & 2 & 1 & 2 & 3 & 4 & 5 & 6 \end{array}\right]$$

Proportion of genes contributed by each age class to future replacements for each Block

$$\tilde{P} = \left[\begin{array}{cc|cccccc} 0 & 1/2 & 0 & 0 & 0 & 0 & 0 & 1/2 \\ 0 & 1/2 & 0 & 1/4 & 1/8 & 1/16 & 1/16 & 0 \end{array}\right]$$

Vector of genetic selection differentials applied to each age

$$s = \left[\begin{array}{cc|cccccc} 0 & 0 & 0 & 0 & 0 & 0 & 1\Delta & 0 \end{array}\right]$$

Computation of uniform rates of response

Genetic selection differentials for each path

$$\left[\begin{array}{c|c} 0 & 1\Delta \\ 0 & 0 \end{array}\right]$$

Weighted parental age groups for each path

$$L = \left[\begin{array}{cc|cccccc} 0 & 1(1) & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1(1) & 0 & \frac{1}{2}(1)+\frac{1}{4}(1.5)+\frac{1}{8}(2)+\frac{1}{8}(2.5)+ & & & & 0 \end{array}\right]$$

Equilibrium rates of response to selection

$$r_{(\infty)} = \left[\begin{array}{ccccccc} 0 & + & 1\Delta & + & 0 & + & 0 \\ 1 & + & 3 & + & 1 & + & 1.44 \end{array}\right]$$

$$r_{(\infty)} = 0.155\ \Delta \text{ (pigs/year)}$$

In Case 1, progeny in B get half of their genes from young boars born in H. The other half of the genes in B come from sows in the base population (B) with some specified age distribution, say 1/2, 1/4, 1/8 and 1/8 of 1, 1.5, 2 and 2.5 year olds, respectively (corresponding to time periods of age classes, 1,2,3 and 4).

In a continuous selection scheme two critical assumptions are made (other assumptions are discussed later). One is that the age structure of the breeding population remains constant in time. The other is that the genetic selection differential also remains constant with repeated selection. As Hill (1974) pointed out there is nothing new in these assumptions since they are implicit in the derivation of the standard equilibrium rates of response to selection. The point will be made clearer when the equilibrium rates are derived by other methods.

V.2.3 Selection

Selection is applied to one path only, for B females to produce progeny in H. Sows in B can be selected with very high intensity (say 1 out of 50, i = 2.42). So the selection differential is applied to B sows producing progeny in H when of age class 6. These sows can be selected on their individual performance on two records (the reference case) with accuracy of selection (r_{HI} = 0.42). The expected genetic selection superiority for selected sows (Δ = $ir_{HI}\sigma_A$) would thus be 0.92 pigs/litter (using the standard parameter values in Table 3.7). For simplicity a value of 1 Δ pig has been used. This could well be achieved by selection on an index including family information (so increasing r_{HI}) or by using even higher intensities of selection.

V.2.4 Response to selection

Equilibrium rates of response to selection

Derivation of the equilibrium rates of response to selection, $r_{(\infty)}$, is straightforward for the examples chosen. Matrix methods of Hill (1974) were used, but as an illustration, Case 1 is derived directly in some detail (Table 5.2). Cases 2 and 3 are summarised in Appendix A5.1. In general, an estimate of $r_{(\infty)}$ is obtained simply as the sum of genetic selection differentials (Δ) applied to each path, divided by the sum of the weighted parental ages contributing to each path. For Case 1 there are only four paths to consider and a selection differential of 1 Δ is applied to one only, namely, that for 3 year old females from B producing progeny in H. Therefore, as shown in Table 5.2, the annual response is $r_{(\infty)}$ = 1/6.438 pigs/litter. Hence, from this table and Appendix A5.1, the equilibrium rates of response to selection are 0.155, 0.087 and 0.047 for cases 1, 2 and 3 respectively. Clearly, the rates of respones with either all, one third or one six of the population bred by sons of hyperprolific females depends to a large extent on the rates of transfer of genes between the nucleus herd and the base population.

V.2.5 Approach to equilibrium

The approach to the equilibrium rates of response should also be considered because of the lags in the hyperprolific selection system. By taking successive powers of **P** (full matrix) and multiplying by a vector (s) of selection differentials, the response, **r**, at year t from one round of selection is obtained. Some correction is needed in the initial stages to account for

ageing (matrix **Q** in Hill, 1974), so that

$$r_{(t)} = (P^t - Q^t)s$$

If selection is continued (constant **s**), the response can be accumulated in time as

$$R_{(t)} = \sum_{T=1}^{t} r_{(T)}$$

Hill (1974) has shown that as $t \rightarrow \infty$, $R_{(t)} - R_{(t-1)}$ approaches the expected equilibrium rates of response.

By this procedure it is possible to follow the initial approach to equilibrium for any part of the system. As an illustration, this is done for the initial build up in genetic merit of nucleus boars available for AI and for the progeny born in the base (B). Tables 5.3 and 5.4 show in detail the initial approach to equilibrium for each case computed, following selection of a single batch of hyperprolific sows. This illustrates that effectively the same values are reached as those derived previously. The same tables also show the build-up of genetic merit in nucleus boars and in the base population progeny, following continuous use of boars from the nucleus and continuous selection of B sows. The build-up in genetic merit of nucleus boars has two phases. The initial phase (assymptotic curve in Figure 5.1) is common to all three cases and lasts until grand daughters of the initial batch of selected sows are themselves selected. Following this, an irregular phase of slow approach to equilibrium follows which is different for each case and dependant on the proportional contributions that nucleus bred boars make to the breeding population B. These results are summarized in figures 5.3, 5.4 and 5.5 for each case respectively.

TABLE 5.3

Response (pigs/litter) from a single selection or from continuos selection of 'hyperprolific' sows with genetic selection differential of 1 pig/litter. The genetic trends are followed in nucleus bred boars (H) and in the base population (B) mated exclusively to boars from the Nucleus (Case 1).

	Nucleus bred boars		Base population
Time (years)	Single selection of hyperprolific sows	Continuous selection of hyperprolific sows	Continued use nucleus boars through AI
0	0.000	0.000	0.000
1	0.500	0.500	0.000
2	0.250	0.750	0.250
3	0.125	0.875	0.469
4	0.063	0.938	0.640
5	0.156	1.094	0.760
6	0.172	1.266	0.904
7	0.164	1.430	1.068
8	0.145	1.574	1.237
9	0.149	1.724	1.394
10	0.154	1.877	1.546
∞	0.155		

TABLE 5.4

Response (pigs/litter) from a single selection or from continuos selection of 'hyperprolific' sows with genetic selection differential of 1 pig/litter. The genetic trends are followed in nucleus bred boars (H) and in the base population (B). Case 2, 1/3 of breeding sows are sired by H boars. Case 3, 1/6 of breeding sows are sired by H boars.

Time (years)	Nucleus bred boars				Base population	
	Single selection of hyperprolific sows		Continuous selection of hyperprolific sows		Continued use nucleus boars through AI	
	Case		Case		Case	
	2	3	2	3	2	3
0	0.000	0.000	0.000	0.000	0.000	0.000
1	0.500	0.500	0.500	0.500	0.000	0.000
2	0.250	0.250	0.750	0.750	0.083	0.031
3	0.125	0.125	0.875	0.875	0.184	0.072
4	0.063	0.063	0.938	0.938	0.285	0.117
5	0.073	0.047	1.010	0.984	0.378	0.161
6	0.082	0.042	1.092	1.026	0.467	0.205
7	0.085	0.041	1.177	1.067	0.555	0.248
8	0.086	0.040	1.263	1.107	0.644	0.291
9	0.086	0.041	1.349	1.148	0.733	0.334
10	0.087	0.041	1.436	1.189	0.823	0.377
∞	0.087	0.041				

FIGURE 5.3 Approach to equilibrium from selection on a continuous hyperprolific scheme. Case 1. All population females mated to nucleus bred boars.

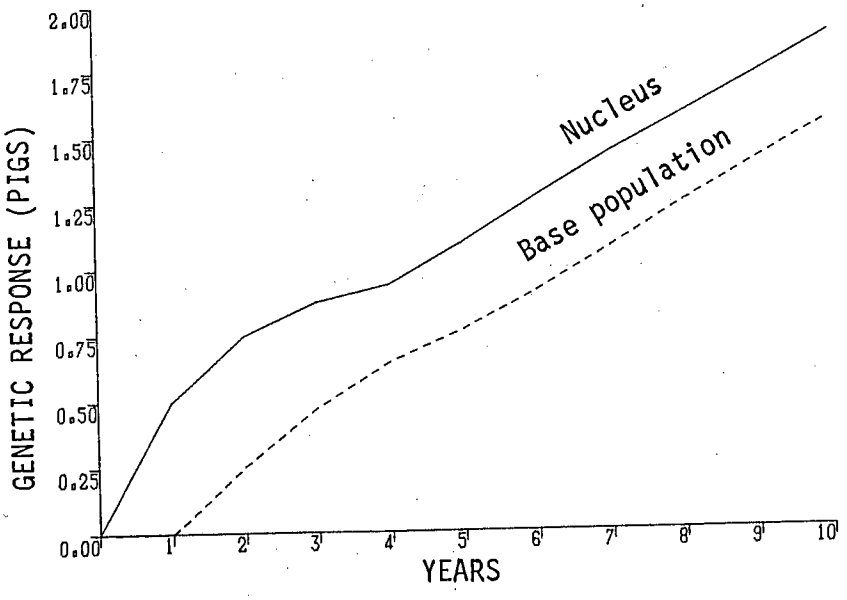


FIGURE 5.4 Approach to equilibrium from selection on a continuous hyperprolific scheme. Case 2. One third of population females mated to nucleus boars.

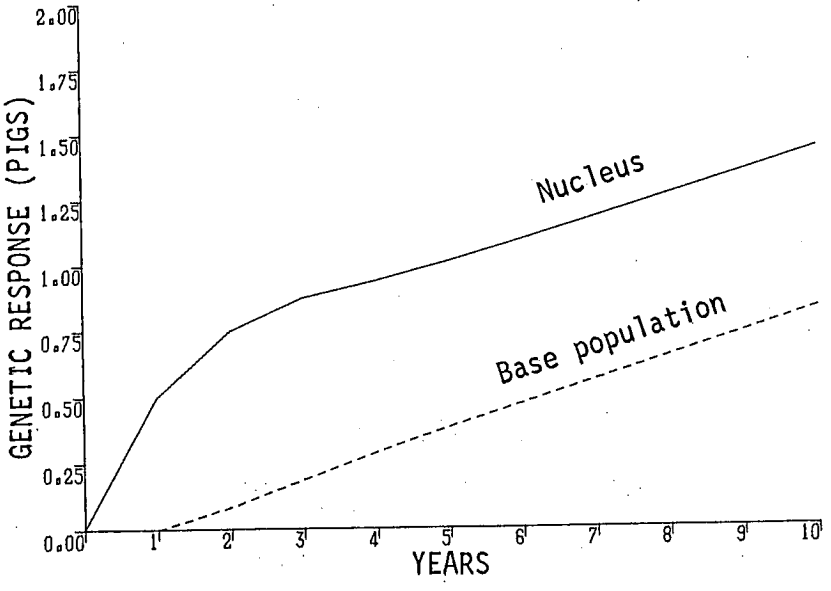
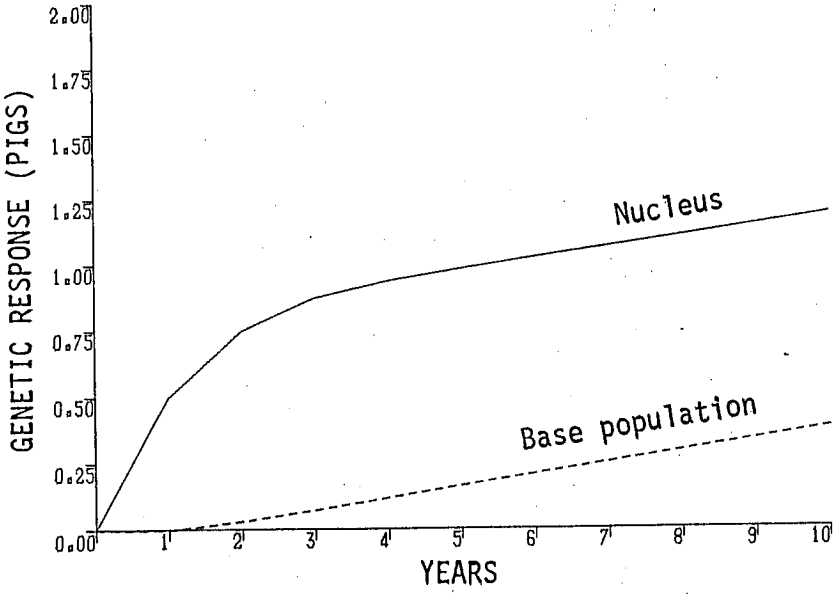


FIGURE 5.5 Approach to equilibrium from selection on a continuous hyperprolific scheme. Case 3. One sixth of population females mated to nucleus boars.



V.3 Hyperprolific dam lines

For a breeding company wishing to improve litter size in a general purpose line or to create a new dam line, adoption of a scheme like that described by Legault and Gruand (1976) might be used (eg. Bichard and Seidel, 1982). However, the procedure would not be without opportunity costs in terms of loss in genetic gain from other economic traits (growth and carcass) currently under selection (lag in the sense used by Bichard, 1971). This is now evaluated in more detail.

V.3.1 Method of selection

The hyperprolific scheme involves very intense selection, so, selection of 1/50 females has been chosen. Consider first selection of females only, with 1) selection on 1, 2, 3 or 4 records of the sow, or alternatively, 2) with one record on the sow plus one record on each of the available sibs, namely, 2 full-sibs (2FS) and 27 half-sibs (27HS) or only 9HS, with the normal family size structures considered earlier. Later, very intense selection is also applied to the males. Selection of 1/50 males can be done on an index using information from relatives, as in Chapter 3. For illustration two indices are used, I_1 with information (two records on each) on the dam (D), her 9 half-sibs (9DHS), one full-sib of the sire (SFS) and his 9 half- sibs (9SHS) plus his dam (SD). The second index, (I_2), considers information on D + 9DHS with two records on each.

V.3.2 Genetic lag in other performance traits.

The minimum genetic lag induced in other performance

traits can be derived for hyperprolific selection schemes as follows:

Assume that batches of hyperprolific sows (H) are selected at regular intervals on (m) records . Each new batch of sows is backcrossed to sons of the previous batch of selected sows. The genetic merit of their progeny will asymptotically reach that of the selected sows (Δ). As before, sows ages (y) are conveniently expressed in 6 month time periods, so age at selection, $y = 1 + m$.

Progeny from hyperprolific schemes will, with repeated backcrossing, have received all their genes from selected H sows. Thus half of their genes will come from H sows age (y), 1/4 from H sows age (y+1), 1/8 from H sows age (y+2), etc. The genetic lag (L) in the progeny will be a direct consequence of the gene contribution from different age groups, namely:

$$L = y/2 + (y+1)/4 + (y+2)/8 + \ldots$$

$$= y(1/2 + 1/4 + 1/8 + \ldots) + (1/4 + 2/8 + 3/16 + \ldots)$$

$$= y(1) + (1/4)[1 + 2/2 + 3/4 + \ldots]$$

$$L = y + 1 \qquad \text{(in 6 month time periods)}$$

$$= (y + 1)/2 \qquad \text{(in years)}$$

As it turns out, lag in this case is only a function of the age of the selected sows. The assumption made for this to be true is that the rest of the population is continuously being selected (i.e.for growth and carcass traits). Therefore, each succesive batch of hyperprolific sows is 'genetically updated' for the other traits.

A useful way to evaluate the merits of going through a hyperprolific scheme for foundation of specialised dam lines is to compare the economic worth of the new line against that of the population of origin, continuously selected for the other traits.

Mitchell, Smith, Makower and Bird (1982) estimated that the pig population in the UK is improving at a rate of £0.76 per year. The most recent estimates from comparisons with control pigs, from 1970 to 1980 is £ 0.68 (C. Smith,personal communication). The relative economic worth (W) of hyperprolific selection has been computed by taking the ratio of the improvement (gain) in litter size (Δ) times its economic value (a_1) over the lag (loss) in growth and carcass traits (L) times the corresponding economic value (a_2), so

$$W = \frac{\Delta a_1}{L a_2}$$

where the a_i's are economic values per unit improvement; a_1 = £2.26 per pig (for specialised dam lines, see chapter 7) and a_2 = £0.68 per year. The break-even point is when W=1, i.e. no gain or loss from the selection procedure.

Results have been derived for the case where progeny from the scheme are used as foundation of a specialised dam line. Extension to general purpose lines merely involves halving the values derived for W, since the economic weights of litter size in general purpose lines is half that in specialised dam lines, as already discussed.

V.3.3 Merit of Scheme

Expected genetic lags and relative economic worth of dam lines from hyperprolific schemes following different methods of selecting females are shown in Table 5.5. Foundation of a specialised dam line with selection of hyperprolific sows on their own records would in most circumstances be worthwhile. The highest relative economic worth of such a dam line with most of the response

in litter size (0.92 pigs per litter) could be achieved by selecting on two litter records (W=1.52). A genetic lag of at least 3 years of selection is expected from schemes selecting on a sow's own 4 records. With one record on self plus 2FS + 27HS or self plus 9HS, a substantial response for litter size is expected, 1.00 or 0.83 pigs per litter making a specialised dam line relatively worth considerably more (2.22 or 1.83 respectively). As could be expected, some improvement (in terms of lag) can be obtained by very intense selection in both sexes. Results are shown in Table 5.6. If records are available, efficiency is increased in all cases. The most efficient method studied is very intense selection of males on an index similar to those described in Chapter 3 and selection of females on an index including own plus sib performance on a single record with an expected improvement of 0.76 or 0.84 pigs per litter. A specialised dam line founded in this manner would be worthwhile (W=2.23 and 2.03 respectively).

TABLE 5.5

Genetic merit[1], lag and relative economic worth, W, of a dam line founded by very intense selection[2] of females with different accuracy, r_f, according to method of selection.

Female selection (Index)	r_f	Lag years	Genetic Merit	W
-Records on self				
4	0.53	3.00	1.15	1.28
3	0.48	2.50	1.05	1.39
2	0.42	2.00	0.92	1.52
1	0.32	1.50	0.70	1.54
-One record on each of				
self + 2FS + 27 HS	0.46	1.50	1.00	2.22
self + 9HS	0.38	1.50	0.83	1.83

[1] $\Delta = i_f r_f \sigma_H$ (pigs/litter)

[2] Selection of 1/50 females, $i_f = 2.42$

$W = \Delta (2.26)/\text{Lag}(0.68)$

TABLE 5.6

Genetic merit[1], lag and relative economic worth, W, of a dam line founded by very intense selection[2] of males and females with different accuracies of selection (r) according to method of selection.

Male selection (index) two records on each of			I_1 D+9DHS+SFS+9SHS+SD		I_2 D + 9DHS	
Accuracy, r_m			0.31		0.24	
Female selection (Index)	r_f	Lag years	Genetic Merit	W	Genetic Merit	W
-Records on self						
4	0.53	2.00	0.92	1.52	0.84	1.39
3	0.48	1.75	0.86	1.63	0.78	1.49
2	0.42	1.50	0.80	1.76	0.72	1.59
1	0.32	1.25	0.69	1.82	0.61	1.62
-One record on each of						
self + 2FS + 27HS	0.46	1.25	0.84	2.23	0.76	2.03
self + 9HS	0.38	1.25	0.75	2.00	0.68	1.80
-Two records on each of						
D+9DHS+SFS+9SHS+SD	0.31	1.00	0.68	2.24	0.60	1.99
D + 9DHS	0.24	1.00	0.60	1.99	0.52	1.74

[1] $\Delta = i(r_m + r_f)\,\sigma_H/2$ (pigs/litter)

[2] Selection of 1/50 males and females, $i_m = i_f = 2.42$

$W = \Delta\,(2.26)/\text{Lag}(0.68)$

V.4 Discussion

With hindsight it is not surprising that a continuous hyperprolific scheme is so inefficient, because of the time it takes for the selected genes to flow through the population. However, none of the schemes have been optimised and it is possible that in some circumstances open nucleus schemes of this sort could be worthwhile (James, 1977). In the long term, open nucleus schemes would probably be useful, especially to capture useful genes at low frequency, including any genes with large effects. In the short term it is difficult to envisage a situation where a continuous hyperprolific scheme would be advisable.

With very intense selection of females only, hyperprolific schemes have been shown to improve litter size (eg. Bichard, 1983a&b, Tomes and Newman, 1982) although Legault, Gruand and Bolet (1981) have not been very successful using national field records. Hence as a method of generating a foundation dam line, such schemes would probably lead to substantial improvement of litter size in most circumstances. Due to lag in other economic traits, the economic worth of lines produced with this method can vary considerably. If family information is available it should be used to increase accuracy of selection, to select both sexes and reduce lag. If very intense selection of males and females can be practiced, the economic rewards from foundation of dam lines would be substantial.

It must be emphasised that the conclusion is probably restricted to the case studied, namely foundation of specialised dam lines. The assumption is that a large recorded population is available, say in multipliers and nucleus, so that, by truncation,

the very best individuals (1/50 hyperprolific) can be used for foundation of a dam line. A useful 'genetic lift' (Δ) is obtained in this way. However, sufficient progeny with m records each must be generated from the new dam line before the same intensity of selection can be applied again and a further Δ achieved. If a second cycle of 'hyperprolific' selection was to be carried out, the benefits (Δ) would need to be spread over the actual period required for development. Take, for example, the case where a foundation dam line is started by selection of 1/50 sows with two records each. Now consider 3 years of backcrossing (for $\Delta \approx 0.70$) and 2 to 3 years for selected sows to generate enough progeny before a second cycle of selection with similar intensity can be carried out. The economic gain from the dam line would need to be spread over 5 to 6 years as well as include development costs. This would need to be compared with continuous and simultaneous improvement of litter size with growth and carcass traits. This point is not pursued any further because there are many possible combinations and it is difficult to generalise. Also, from theory it is expected that index selection will be more efficient in improving overall economic value following the same model assumptions (Falconer, 1981).

Finally, all the discussion has been in terms of lag. As pointed out earlier, another consideration is the actual time needed to develop a new dam line. In the example used previously, the time required could be between 5 and 6 years. Whereas some of the results of tables 5.5 and 5.6 are not very different in terms of lag and W, it is worth pointing out that the development time required for the latter is only one year.

CHAPTER VI. PROGENY TESTING

VI.1 Selection system

Some countries, like Norway and Finland, have large recorded populations of sows bred by artificial insemination (AI). Under these circumstances, a selection system based on progeny testing can be used. Progeny testing is specially suited for traits which are sex limited to females, are expressed after reproductive age and have low or moderate heritability. The progeny test provides a direct measure of a sire's breeding value. However, the accuracy of estimation depends on the number of daughters and on fair unbiassed comparisons of progeny groups. The selection of males on progeny test results, at 3 years, will increase the generation interval for the whole selection system. Selection must thus be accurate and selection intensities high in order to counteract the effect of the longer generation interval on the predicted annual rates of response to selection.

Progeny testing for litter size has been evaluated previously. Ollivier (1974) considered a selection system based on progeny testing boars without any selection on females. More recently Leukkunen (1984) evaluated selection of females on an index combining their own litter size and their sire's progeny test results, and selection of males on progeny test. Here the selection effort has been directed at three levels; at candidate males (1) and females (2) selected for breeding on an index within a nucleus herd, and the progeny test of males (3), selected from the first stage of selection. The system has been designed to select the optimum proportion of nucleus born males by progeny testing with

optimum progeny group sizes for fixed testing resources.

VI.2 Selection herd

Consider a nucleus selection herd like that in Chapter 3. It is the genetic improvement in this herd that is considered, and so the AI bred sow population serves as a testing population for progeny testing young males from the nucleus herd. The selected progeny tested sires are then used in the nucleus herd. Of course, any genetic trends in the nucleus herd are gradually passed on to the AI bred sow population through the use of the next generation of selected young males, or by reuse of the progeny tested sires. The total number (T) of recorded daughters of boars being progeny tested depends on the size of the population of females, and the proportion of these allocated to young boars. To minimise the generation interval for males only first litter records will be used in the progeny test, so only about a quarter of the sows (at one time) will provide records on the current batch of boars being progeny tested. In practice, for replacement, on average one female per litter will be retained, so the progeny groups will be mainly half-sib groups. It is assumed that sows are allocated at random among the boars being tested.

VI.2.1 Female selection

Females in the nucleus herd are selected as before on an index. However their sires are progeny tested boars of an earlier batch. With intense and accurate selection of these sires, they will be similar in genetic merit so there will be little information from the sire path. Thus the index I_3 derived for the dams

relatives in Chapter 3, is used for female selection here.

VI.2.2 Male selection

Nucleus born males are selected in two stages:

a) First stage selection, a proportion (p_1) of young males is selected on the same index as the females (I_3).

b) Second stage selection, a proportion (p_0) of boars is selected on progeny test results.

The schedule considered for the progeny testing of boars is shown in Table 6.1. Candidates for progeny testing are taken from first litters of nucleus females and after selection on progeny test results are used in the nucleus. Their nucleus progeny are born when boars are 35-37 months old, giving a generation interval for males (L_m), of on average 3 years.

VI.3 Size of selection herd

For the same reasons as in the previous section, the size of the nucleus herd will be set to limit the annual rates of inbreeding to 0.0025. With $L_f = 1$ and $L_m = 3$, the average generation interval is $L = 2$. For the mating ratio used (1/10), the number of sires per year required is then aproximately 12. Thus a nucleus herd of 12 males and 120 females would be required. A further 240 unselected female relatives need to be kept in other recorded herds if all the information proposed for the index is to be available.

VI.3.1 Size of testing facilities and optimum use

Three sizes of populations of AI sows have been considered (25, 50 and 100 thousand). If all females in the base were bred by

TABLE 6.1

Schedule for progeny testing schemes of males selected on the litter size performance of their daughters.

Nucleus	Progeny testing (ie national herd)	Months
Males born		0
Semen available+	mating	7-12
	daughters born	11-16
	daughters 1st mating	18-23
	daughters farrow	22-27
Male selection	records available	28-30
Top males mated to nucleus females		31-32
Progeny born		35-37
Generation interval (L_m) in years		3

+10 doses, 5 inseminations and 3.5 conceptions per week, providing an average of 3.5 recorded daughters (1 per litter) per week and 91 over a 6 month period.

(Recent MLC figures)

young boars being progeny tested, about 1/4 will be one year old and daughters of the latest batch of young sires. This represents the totals (T) for testing, 6.25, 12.5 and 25 thousand respectively. With a requirement of 12 progeny tested boars (S) for nucleus replacements, the optimum proportion (p_0) of nucleus males selected

and the optimum progeny group sizes (n_0) that will maximise the expected genetic superiority of sires can be derived. The following approximate formulae of Robertson (1957) were used

$$K = T/S$$

and

$$n_0 = 0.56(K/h^2)^{1/2}$$

The optimum proportion of boars to test (p_0) is approximately

$$p_0 = 0.28(a/K)^{1/2}$$

where

$$a = (4-h^2)/h^2$$

The same reference parameter values have been used as before, and the same nucleus mating ratio (1:10).

Given the nucleus size (with d sows and n progeny per sow), and testing facilities specified, there will sometimes be more male progeny available (nd) than those required to test and select the optimum proportion (p_0). In those cases studied where $nd>1/p_0$, a proportion $p_1=1/ndp_0$ would be selected on I_3 (first stage selection) prior to progeny testing (second stage selection).

VI.4 Accuracy of selection

The accuracy of selection for females using index I_3 is $r_1 = 0.273$ as derived in Chapter 3. The accuracy of the initial selection of males is the same. The effect of the initial selection on the genetic variation available at the second stage needs to be taken into account. Following Robertson (1977), the variance component within progeny groups (6^2_W) is unaffected by

previous selection. The variance component between progeny groups (σ^2_S) is reduced by a factor kr_1^2. So the variance component between progeny groups of boars selected in stage one is

$$\sigma_{B'}^2 = \sigma^2_B(1-kr_1^2) = (1/4)VA(1-kr_1^2)$$

where

$$k = i_1(i_1 - x)$$

and x is the normal deviate corresponding to p_1.

The variance of half-sib progeny family (n) means of boars selected in stage one is then (V_{hs}).

$$V_{hs} = \sigma_B^2(1-kr_1^2) + \sigma_W^2/n$$

after substituting and rearranging

$$V_{hs} = [VP - (1/4)VA(n(1-kr1^2)-1)]/n$$

The correlation of progeny means with breeding value of selected boars (r_2) is

$$r_2 = [\sigma^2_{B'}/(\sigma^2_{B'} + \sigma^2_W/n)]^{1/2}$$

which after substituting and rearranging is

$$r_2 = [(1/4)h^2n(1-kr_1^2)/(1 + (1/4)h^2(n(1-kr_1^2)-1))]^{1/2}$$

If there is no previous selection (first stage) then by substituting k = 0 gives the usual formula

$$r_2 = [(1/4)h^2n/(1 + (1/4)h^2(n-1))]^{1/2}$$

VI.5 Selection response

The expected annual rates of response to selection for litter size can now be derived by putting together the contributions (R) from the different paths and stages of selection.

$$R = R_f + R_{m1} + R_{m2}$$

where

$$R_f = i_f r_1 \sigma_A / (L_m + L_f)$$

$$R_{m1} = i_{m1} r_1 \sigma_A / (L_m + L_f)$$

$$R_{m2} = i_{m2} r_2 \sigma_A \ (1-kr_1^2)^{1/2} / (L_m + L_f)$$

VI.5.1 Female selection

Selecting 1 out of 3 females on index (I_3) with $i_f = 1.1$ and $r_1 = 0.27$, gives and annual genetic response for this path (R_f) of 0.07 pigs (Table 6.2).

TABLE 6.2

Parameters and annual rates of response to selection predicted from female selection with a nucleus on an index. 1. Female path.

Generation interval in years (summed for males and females)	4.25
Proportion selected	1/3
Standardised selection differential (i_f)	1.1
Mating ratio (males/females)	1/10
Accuracy of selection (r_1)	0.27
Rates of response to selection (R_f) from this path	
in pigs	0.07
in genetic standard deviation units	0.07

VI.5.2 Single stage selection of males (progeny test only)

Consider first no selection of males in stage one. For the three sets of testing resources considered corresponding to populations of 25, 50 and 100 thousand sows, with optimum progeny

testing schemes, responses of 0.30, 0.35 and 0.40 pigs per annum could be achieved (Table 6.3). Adding female selection response the total genetic response for this combination rises to 0.37, 0.42 and 0.47 pigs per year. This represents an increase of 23, 20 and 18 percent respectively over the expected rates of response for an optimum progeny testing scheme on its own.

TABLE 6.3.

Parameters and annual rates of response to selection predicted from male selection on progeny test alone. 2. Male path.

Generation interval in years (summed for males and females)	4		
Size of AI population (thousands)	25	50	100
Proportion of males selected	1/13	1/18	1/26
Standardised selection differential	1.88	2.02	2.17
Optimum progeny group size	40	57	81
Accuracy of selection (r_2)	0.71	0.77	0.82
Annual rates of response to selection (R_{m2}) from this path			
in pigs	0.30	0.35	0.40
in genetic standard deviations	0.33	0.39	0.45

VI.5.3 Two stage selection of males (index + progeny test)

For each of the testing resources, the number of young males in the nucleus herd exceeds the number required to select the optimum proportions on progeny test. So, an initial selection of males on an index is carried out. The results are given separately for each stage of selection in Table 6.4. The expected responses

TABLE 6.4

Parameters and annual rates of response to selection predicted from male selection on a nucleus and AI index progeny test.
3. Male path

Generation interval in years (summed for males and females)	4		
Size of AI population (thousands)	25	50	100
First stage selection			
Proportion of males selected (p_1)	0.44	0.62	0.87
Selection differential (i_{m1})	0.90	0.61	0.24
Accuracy of index (r_1)	0.27	0.27	0.27
Annual rates of response to selection (R_{m1}) from this path			
in pigs	0.06	0.04	0.01
in genetic standard deviations	0.06	0.04	0.02
Second stage selection (progeny test)			
Proportion of males selected (p_0)	1/13	1/18	1/26
Selection differential (i_{m2})	1.88	2.02	2.17
Optimum progeny group size (n_0)	40	57	81
Accuracy of selection (r_2)	0.72	0.78	0.83
Annual rates of response to selection (R_{m2}) from this path			
in pigs	0.30	0.35	0.40
in genetic standard deviations	0.33	0.39	0.44

from the first stage of selection are 0.06, 0.04 and 0.01 pigs per year for each of the testing resources. The second stage selection of males on progeny test would increase this by 0.30, 0.35 and 0.40 pigs per year. Adding the female path brings the total expected responses to 0.42, 0.45 and 0.49 pigs per year respectively.

The expected annual genetic responses to selection for litter size in genetic standard deviation units are shown for comparison in Table 6.5 for the different alternatives of selection.

TABLE 6.5

Expected annual rates of response to selection for litter size (in genetic standard deviation units) summed over paths from Tables 6.2, 6.3 and 6.4).

Size of AI population (thousands)		25	50	100
Method of selection				
Males	Females			
Progeny test	None	0.33	0.39	0.45
Progeny test	Index (I_3)+	0.41	0.47	0.53
(I_3) + Progeny test	Index (I_3)	0.47	0.50	0.54
Index (I_6)++	Index (I_6)		0.52	

+ Table 3.4
++ Table 3.8

VI.6 Discussion

With a large AI bred and litter recorded sow population, this nucleus herd - AI progeny testing selection system should be an efficient means of increasing litter size in pig populations. Ollivier (1974) found progeny testing of boars gave 17% to 35% less response than selection of both sexes on the dam's first two litters. For the same base population parameters, simple progeny testing of boars gave responses 11% to 51% superior in the cases studied here. With combining the three paths, this selection system would be 58% to 81% superior to selecting on dam's first two litters. Leukkunen (1984), on the other hand, compared selection on a sow's own performance for one litter (1), with (1) plus her sire's progeny test (2), and (2) plus mild selection of boars on their own progeny test results (3). The relative efficiency of the three was 100, 118 and 160 respectively. Compared to selection on a dam's two records, however, all were substantially inefficient.

The maximum genetic response came from the system with two stage selection of males. For each of the testing resources, the total expected responses amounted to 0.42, 0.45 and 0.49 pigs respectively. This represents a moderate improvement of 14, 7 and 4 percent over the case with single stage selection. More importantly perhaps is the reduction in the difference between the two extreme sets of testing resources. The initial difference of 33% between the extremes for a 4-fold difference in T on progeny test selection alone is halved to 16% when two stage selection is considered. Thus, the schemes involving progeny testing from a selection nucleus herd can yield responses similar to those derived

previously with the full family index (I_6). However with progeny testing the generations overlap and a small correction for the initial lag should be included in the calculations. It has been assumed that unbiassed estimates of sire progeny means are available. Two possible sources of bias are pedigree errors and non-random allocation of females to boars. In assessing the accuracy it will be the number of effective daughters (depending on the number of contemporaries) rather than the actual number of daughters which should be used. Some of these factors may reduce the expected rates of response.

CHAPTER VII COMBINED INDEX

VII.1 Selection system

In practice it is unlikely that selection would be for litter size alone. Rather the selection objective will be to maximise overall economic genetic response, considering growth and carcass traits as well as reproductive performance. In this section a combined selection index is derived and the importance of litter size in this index is evaluated. Selection will be for both general purpose stocks and for specialised dam (maternal) stocks.

For growth and carcass traits the parameters from the current MLC (Meat and Livestock Commission) pig selection index were used, as presented by Cook (1977). For litter size the material and methods are the same as in Chapter 3. In the performance test, results for growth and carcass traits are available before breeding age. Candidates for selection can thus be selected for these traits and for litter size on family records at the same time. So, a generation interval of one year is also quite feasible.

In the MLC combined test, a test group consists of two boars and a sib pair (castrate and gilt) from the same litter. The recorded traits taken on a test group are shown in Table 7.1. Daily gain, food conversion ratio and ultrasonic fat depth are measured for each boar (traits 1-3). For the sib pair, the pair's average daily gain and food conversion are recorded (traits 4-5). After slaughter the pair average for carcass fat depth, killing out percent, trimming percent, eye muscle area (L. dorsi) are taken (traits 6-9). Finally lean percent is estimated in one of the sibs, on a joint or half carcass dissection (trait 10).

TABLE 7.1

Records taken on each MLC combined test group and included in the performance test index for boars and litter size records also available for selection.

Recorded trait	Measurement	Symbol	Units
	Individual boars		
1	Daily gain	DB	g/day
2	Food conversion ratio	FB	food/gain
3	Backfat depth (ultrasound)	UB	mm
	Sib average		
4	Daily gain	DS	g/day
5	Food conversion ratio	FS	food/gain
6	Carcass backfat depth (caliper)	BF	mm
7	Killing out percent	KP	%
8	Trimming out percent	TP	%
9	Eye muscle area	EM	cm^2
10	Lean percent	LP	%
	Family litter records		
11	Dam	D	pigs/litter
12	Dam full-sibs	DFS	pigs/litter
13	Dam half-sibs	DHS	pigs/litter
14	Sire full-sibs	SFS	pigs/litter
15	Sire half-sibs	SHS	pigs/litter
16	Dam of sire	DS	pigs/litter

VII.2 Combined selection index

To derive the combined selection index including litter size, the economic value for each selection trait is required. These are taken from the MLC index and are shown in Table 7.2. Other economic values are shown for comparison. The economic value for litter size has been calculated on a per pig basis, to bring it into line with the other traits, and depends in the savings in sow costs per extra pig per litter. Details are given in Table 7.3.

TABLE 7.2

Selection traits, and their economic values (a) in pence/unit for the aggregate breeding value (H).

Reference year			(1983)[1]	(1977)[2]	
	Selection trait	Units	value	value	Symbol
1	Daily gain	g/day	.97	.70	DG
2	Food conversion	food/gain	-1073	- 864	FC
3	Killing out percent	%	87	63	KP
4	Dressing percent	%	65	53	DP
5	Eye muscle area	cm^2	3	3	EM
6	Lean percent	%	55	55	LP
7	Litter size[3]	pigs	113	135	LS

1. From Guy, personal communication
2. From Mitchell et al. (1982)
3. Estimated on a per pig basis as savings in sow costs per extra pig born (see Table 7.3)

TABLE 7.3

Costs in reproduction and derivation of economic weights for litter size (from Guy, personal communication).

Item	Symbol	Constants
Food consumed		
- While lactating+	F_1	5kg/day
- While dry	F_2	2.5kg/day
Days per lactation	d_1	35 days
Lactations per year	d_2	2.1
Average litter size	$\bar{x}$	10
Costs		
Sow feed costs	e_s	£0.14/kg
Non feed costs		
- variable (fuel, vet, etc)	e_v	£22/year
- fixed (buildings, labour, etc)	e_f	£63/year

+ Independent of litter size

Derivation of sow costs per litter (D)

$$D = [e_s[(F_1-F_2)(d_1.d_2) + F_2(365)] + e_v+e_F]/d_2$$

Derivation of the value (V) of extra piglet (on a per pig basis)

$$V = \frac{D}{\bar{x}} - \frac{D}{\bar{x}+1} = \frac{D}{\bar{x}(\bar{x}+1)}$$

$$V = \frac{D}{\bar{x}^2} \quad \text{(approximately)}$$

Substituting

$$D = (153 + 22 + 63)/2.1 = 113$$

$$V = £1.13$$

The economic weight derived for litter size applies to stocks used as purebreds, in rotational crossing or in reciprocal crosses. These stocks will be called general-purpose stocks. If a stock is used as a dam or maternal line, then the economic weight given to litter size can be doubled, or alternatively the economic weights given to non reproductive traits can be halved (Smith, 1964). This is because specialised dam lines express their full merit for reproduction, but contribute only half of the growth and carcass trait genes to their commercial crossbred (slaughter generation) progeny. In specialised sire lines, often called terminal sire lines, little or no economic weight need be given to female reproductive performance, so inclusion of litter size will not be worthwhile in such lines.

The aggregate breeding value combining the six MLC index traits and litter size is:

$$H = \sum_{i=1}^{7} a_i G_i$$

where a_i are the economic weights and G_i the breeding values for the seven selection traits.

The combined selection index is derived by solving the equations

$$\mathbf{Pb = Ga}$$

The phenotypic variance covariance matrix includes the 10 traits recorded in the MLC combined test, and the 6 litter size sources for index I_6 (Chapter 3). For simplicity it is assumed that the performance traits are uncorrelated, both phenotypically and genetically, with litter size (Morris, 1975). The phenotypic variances and covariances for the 10 recorded performance traits

are simply the estimates observed in the MLC test data (Cook, 1977). For litter size, they are those given for deriving I_6.

There is a complication in defining the aggregate breeding value and in deriving the G covariance matrix. The genetic correlation between performance of the same trait in different sexes often seems to be less than one (Cook, 1977), so the proportion of the different sexes among commercial slaughtered pigs must be taken into account. Cook (1977) used the ratio of boars : castrates : gilts of 2:3:3 implying that a proportion 0.4 of gilts were retained for breeding. The proportion of pigs slaughtered as boars is thus 0.25, and 0.75 for non-boars (sibs). The breeding value for the i^{th} selection trait can be subdivided into boars (B) and sibs (S) as

$$G_i = (1/4)G_{iB} + (3/4)G_{iS}$$

The covariances of recorded traits (1-10) and selected traits (1-6) can then be derived as

$$CovP_iG_j = (1/4)CovP_iG_{jB} + (3/4)CovP_iG_{jS}$$

The genetic covariances (and variances) for the selection traits (1-6) are

$$CovG_iG_j = (1/16)[CovG_{iB}G_{jB} + 3CovG_{iB}G_{jS} + 3CovG_{iS}G_{jB} + 9CovG_{iS}G_{jS}]$$

These were evaluated from estimates of the parameters presented by Cook (1977) and are given in Tables 7.4-7.7. Some of the covariances were not available, for example $CovG_{1B}G_{4B}$, since selection trait 4 (dressing percent) was not available for boars but only for their sibs. Three alternative cases were studied, setting

1. $Cov\ G_BG_B = Cov\ G_BG_S$
2. $Cov\ G_BG_B = Cov\ G_SG_S$
3. $Cov\ G_BG_B = Cov\ G_BG_S = Cov\ G_SG_S$

The third case implies a genetic correlation among sexes of one for the same trait, and an equal genetic correlation among sexes for different traits.

TABLE 7.4

Phenotypic and genetic covariances of recorded traits (1-3) for boars.

Recorded traits		Covariance		Symbols
		Phenotypic	Genetic	
1	1	2039.430	446.634	DB,DB
1	2	-6.872	-1.931	DB,FB
1	3	-31.359	-61.397	DB,UB
2	2	0.036	0.010	FB,FB
2	3	0.429	0.336	FB,UB
3	3	301.370	100.356	UB,UB

TABLE 7.5

Phenotypic and genetic covariances between boar (1-3) and sib (4-10) recorded traits.

Recorded traits		Covariance		Symbols
		Phenotypic	Genetic	
1	4	322.874	245.335	DB,DS
1	5	-1.076	-0.962	DB,FS
1	6	-1.702	-3.403	DB,KP
1	7	0.289	-0.640	DB,TP
1	8	1.955	-4.779	DB,EM
1	9	2.942	-2.351	DB,LP
1	10	-31.861	-52.876	DB,BF
2	4	-1.274	-1.572	FB,DS
2	5	0.006	0.007	FB,FS
2	6	0.005	0.018	FB,KP
2	7	-0.002	0.002	FB,TP
2	8	-0.016	0.015	FB,EM
2	9	-0.042	-0.062	FB,LP
2	10	0.323	0.410	FB,BF
3	4	-38.650	-13.682	UB,DS
3	5	0.288	0.353	UB,FS
3	6	1.793	3.796	UB,KP
3	7	0.321	0.438	UB,TP
3	8	-1.698	-0.267	UB,EM
3	9	-10.287	-13.654	UB,LP
3	10	93.585	125.322	UB,BF

TABLE 7.6

Phenotypic and genetic covariances among sib recorded traits (4-10).

Recorded traits		Covariance		Symbols
		Phenotypic	Genetic	
4	4	1861.490	518.116	DS,DS
4	5	-4.809	-1.968	DS,FS
4	6	-7.164	1.294	DS,KP
4	7	2.602	0.842	DS,TP
4	8	8.585	2.120	DS,EM
4	9	17.139	26.595	DS,LP
4	10	-102.867	-74.474	DS,BF
5	5	0.023	0.013	FS,FS
5	6	0.029	0.012	FS,KP
5	7	-0.009	-0.006	FS,TP
5	8	-0.058	-0.067	FS,EM
5	9	-0.181	-0.247	FS,LP
5	10	1.300	1.270	FS,BF
6	6	1.632	0.897	KP,KP
6	7	0.124	0.134	KP,TP
6	8	0.488	0.315	KP,EM
6	9	-0.340	-0.290	KP,LP
6	10	5.245	4.376	KP,BF
7	7	0.246	0.113	TP,TP
7	8	0.191	0.210	TP,EM
7	9	0.125	0.047	TP,LP
7	10	0.033	0.518	TP,BF
8	8	2.534	1.769	EM,EM
8	9	1.977	2.405	EM,LP
8	10	-10.595	-11.521	EM,BF
9	9	9.103	7.737	LP,LP
9	10	-42.960	-46.575	LP,BF
10	10	394.754	370.410	BF,BF

TABLE 7.7

Genetic variances and covariances among the selection traits (1-7) in the aggregate genotype (H).

Traits in H		Sex interactions: no	no	yes	
		Case 1	Case 2	Case 3	Symbols
1	1	411.355	411.355	403.362	DG,DG
1	2	-1.703	-1.703	-1.722	DG,FC
1	3	-0.761	-0.467	-1.055	DG.KP
1	4	0.194	0.286	0.101	DG,TP
1	5	-0.899	-0.467	-1.055	DG,EM
1	6	13.929	15.738	12.121	DG,LP
1	7	0.000	0.000	0.000	DG,LS
2	2	0.011	0.011	0.010	FC,FC
2	3	0.015	0.014	0.015	FC,KP
2	4	-0.003	-0.003	-0.002	FC,TP
2	5	-0.031	-0.036	-0.026	FC,EM
2	6	-0.166	0.178	-0.155	FC,LP
2	7	0.000	0.000	0.000	FC,LS
3	3	0.897	0.897	0.897	KP,KP
3	4	0.134	0.134	0.134	KP,TP
3	5	0.315	0.315	0.315	KP,EM
3	6	-0.290	-0.290	-0.290	KP,LP
3	7	0.000	0.000	0.000	KP,LS
4	4	0.113	0.113	0.113	TP,TP
4	5	0.210	0.210	0.210	TP,EM
4	6	0.047	0.047	0.047	TP,LP
4	7	0.000	0.000	0.000	TP,LS
5	5	1.769	1.769	1.769	EM,EM
5	6	2.405	2.405	2.405	EM,LP
5	7	0.000	0.000	0.000	EM,LS
6	6	7.737	7.737	7.737	LP,LP
6	7	0.000	0.000	0.000	LP,LS
7	7	0.810	0.810	0.810	LS,LS

VII.3 Sensitivity of the index to sex interactions

Before analysing the value of including litter size in a combined index, the sensitivity of the index to imperfect genetic correlations between sexes is considered. Since the performance traits are assumed to be uncorrelated with litter size, it is possible to assess the effect on the performance test index on its own within the same framework. The results are shown in Table 7.8. No single recorded trait dominates the index, except for boar's backfat depth in Case 3, accounting for almost 20% of the index's efficiency. Most of the economic benefit is by improvement of food conversion ratio and lean percent. The three indices differ substantially in accuracy of selection, due to the imperfect genetic correlation among sexes in cases 1 and 2. The relative rates of estimated genetic response from the same selection intensities are 100, 111 and 142 respectively for cases 1, 2 and 3. The difference of 42% between cases 1 and 3 represents the expected loss in genetic response due to the imperfect genetic correlation among sexes.

VII.4 Value of litter size in selection

Pig selection in the UK has been based on an aggregate breeding value of six growth and carcass traits, and on an index I* of 10 recorded traits (Cook, 1977). The correlation of this index with **H**, the aggregate breeding value for seven selection traits, including litter size (Table 7.2), measures the accuracy of I* in selection to improve overall economic merit. This value has been computed for assumed general purpose and specialised dam lines (Table 7.9). It forms the basis to estimate the relative value of including litter size information.

TABLE 7.8

Sensitivity of the performance trait index to imperfect genetic correlations among sexes. Index weights (b_i), value of recorded traits, regressions of each selection trait on index (b_{GiI}), percent of total gain (or loss) from each trait, correlation of index with aggregate genotype ($r_{I,H}$) and standard deviation of index (o_I).

			Sex interactions				No sex interaction	
Recorded trait			Case 1		Case 2		Case 3	
			b_i	Value (%)	b_i	Value (%)	b_i	Value (%)
Boar	DB	1	-0.01	2	-0.01	1	-0.01	1
	FB	2	-3.97	7	-4.31	7	-5.70	8
	UB	3	-0.02	3	-0.03	8	-0.06	19
Sibs	DS	4	0.00	0	0.00	0	0.00	0
	FS	5	-2.99	3	-2.96	2	-2.25	1
	BF	6	0.00	0	0.00	0	0.02	2
	KP	7	0.19	2	0.19	2	0.14	1
	TP	8	0.10	0	0.11	0	0.11	0
	EM	9	0.13	1	0.13	1	0.15	1
	LP	10	0.13	5	0.13	4	0.16	4

Selection trait	G_i	b_{GiI}	Gain (%)	b_{GiI}	Gain (%)	b_{GiI}	Gain (%)
DG	1	5.18	5	4.89	5	4.30	4
FC	2	-0.04	41	-0.04	38	-0.04	38
KP	3	-0.02	-2	-0.06	-5	-0.08	-7
TP	4	0.02	1	0.01	1	0.01	1
EM	5	0.25	0	0.29	0	0.31	0
LP	6	0.99	54	1.12	61	1.18	65

Case 1, Cov G_BG_B = CovG_BG_S, Case 2, Cov G_BG_B = Cov G_SG_S

Case 3, Cov G_BG_B = Cov G_BG_S = Cov G_SG_S

Value = Percent loss in accuracy (or response) from omitting each recorded trait

TABLE 7.9

Accuracy of indices ($r_I{}^*{}_H$) for selecting pigs on an aggregate genotype of seven traits which includes litter size with varying economic weight but ignoring litter size among the recorded traits in (I^*).

		Sex interactions		No sex interaction
		Case 1	Case 2	Case 3
Value of litter size		$r_I{}^*{}_H$	$r_I{}^*{}_H$	$r_I{}^*{}_H$
	£0.00	0.47	0.52	0.67
General lines	£1.13	0.44	0.48	0.62
Dam lines	£2.26	0.36	0.40	0.51

Case 1, Cov G_BG_B = CovG_BG_S, Case 2, Cov G_BG_B = Cov G_SG_S

Case 3, Cov G_BG_B = Cov G_BG_S = Cov G_SG_S

It is now possible to assess the value of including litter size in the selection index. The accuracy of selection with an index of 10 recorded growth and carcass traits (I_{10}) is compared with the accuracy of selection adding the dams litter size (I_{11}) the dam's family (I_{13}) and both the dam's and sire's families (I_{16}). The relative efficiencies of selection using varying amounts of information for litter size are given in Table 7.10.

For general purpose lines, gains in accuracy of selection of only two to five percent are obtained by including litter size in the index. In each case, as more litter size information is added, the accuracy is increased a little. With no sex interaction (case

3), the gains are lower since the accuracy of selection for growth and carcass traits is higher. Larger gains in accuracy, up to 19 percent, would be obtained in specialised dam lines.

The derivation and handling of the variance-covariance matrices was often rather complex due to the sex interactions and differences in recorded and selected traits. Numerical and logical errors might have been made. A check on the results was made by dealing with a simple set of parameter estimates and ignoring the sex interactions.

TABLE 7.10

Relative efficiency of selection for the aggregate breeding value of seven selection traits with performance traits alone (I_{10}) and with litter size added. a) General purpose lines. b) Specialised dam lines.

	Sex interaction								No sex interaction			
	Case 1				Case 2				Case 3			
Index	I_{10}	I_{11}	I_{13}	I_{16}	I_{10}	I_{11}	I_{13}	I_{16}	I_{10}	I_{11}	I_{13}	I_{16}
General lines	100	102	103	105	100	102	103	104	100	101	102	103
Dam lines	100	107	111	119	100	106	109	115	100	104	106	110

I_{10} Index of 10 recorded growth and carcass traits

I_{11} Above plus dams litter records

I_{13} Above plus dams full- and half-sib litter records

I_{16} Above plus sire family records

VII.5 Discussion

An important assumption has been that litter size is independent, both phenotypically and genetically, of growth and carcass traits. Hill and Webb (1982) give a summary of estimates of genetic correlations from two analyses (Table 7.11). However the standard errors are very high, and only the unfavourable correlation with killing out percent (1 out of 16 estimates) is significantly different from zero. Experimental evidence from pig selection lines, for high and low fat depth (Hetzer and Miller, 1970) and for high growth rate with low fat depth and vice versa (Vangen, 1980), show little change in litter size. In the absence of much evidence to the contrary, it seems reasonable to use (a priori) a genetic correlation of zero for litter size with growth and carcass traits. However, it might be noted that if the average values for the genetic correlations given in Table 7.11 are used in the index derivation, the relative value of including litter size in the index drops appreciably due to mostly favourable genetic correlations.

Other factors affect the value of including litter size in the selection index. It has been shown that if sex interactions are important, reducing the accuracy (or value) of selection for growth and carcass trait, then the value of including litter size increases. Alternatively reducing sow costs, for example by considering only the costs during gestation, and not in rearing, would reduce the value of including litter size.

TABLE 7.11

Genetic correlations (%) between growth and carcass traits and litter size at birth (From Hill and Webb, 1982).

Source	Morris (1975)[1]		Legault (1971)[2]
Breed	Large White	Landrace	Large White
Trait			
Daily gain	6	44	-8
Food conversion ratio	-15	-21	8
Killing out %	-63	-49	-
Backfat	-18	-36	11
Hindquarters %	-41	-12	-
Ham and loin %	-	-	2
Total index points	1	-4	-

[1] SE's 30% for Large White, 45% for Landrace
[2] SE's not given or not significant

It could be argued that family information should be used for all traits and not only for litter size to make comparisons fair. Strictly speaking this is true but would make calculations much more complicated, especially if taking account of sex interactions. This omission is not considered serious. First, the relative improvement from additional family information in the accuracy of selection for growth and carcass traits is expected to be much smaller than for litter size due to the higher heritabilities of the component traits of the former. Also, it is not difficult to see the effect of including family information for growth and carcass traits (G + C) since these are treated as independent from litter size (LS). The ratios of the accuracies of

selection (G + C):LS would need to be at least 4:1 for there to be no value in including litter size in the index.

With the systems and parameters described, including litter size in a combined selection index can improve the economic efficiency of pig meat production. However the extra benefit in general purpose lines will be rather small (2-5 percent). For specialised dam lines, larger gains (10-19 percent) would be expected, and these would seem worthwhile aiming for.

These results are at first somewhat surprising in view of the large percentage (4.6 per year) changes in litter size estimated in Chapter 3, and the high economic weight for litter size (Table 7.2). However the effects of the higher heritabilities and cumulative economic weights of the other traits outweigh the effect of litter size in the selection index. This might have been predicted from the results for index selection of Smith (1983).

Past selection work in the UK has largely ignored selection for litter size. The present results show that this was probably reasonable, specially since the stocks were mostly used as general purpose lines. With the development of specialised dam lines, it would seem important to include litter size in the selection index, and this is worthwhile and recommended.

CONCLUDING REMARKS

Up till now it has been generally accepted that little response to selection for litter size in pigs is to be expected. The reasons most commonly given are its low heritability, that it can only be measured in females, and only after reproductive age. Yet here the rates of response in litter size from selection on a family index are estimated to be as high as 4 to 6 percent of the mean per year. These are substantial rates and are in fact much higher than estimates for much more heritable traits. Such high rates of response for litter size in pigs are possible because of its high coefficient of variation, the availability of records on many relatives and the short generation interval. These advantages more than compensate for the disadvantages cited earlier. Such impressive rates are, with present knowledge, quite possible with only minor reservations as discussed subsequently.

Recent reports of negative maternal effects and disappointing experimental selection results have given some cause for concern. In particular, it has been argued that the efficiency of selection for litter size may be reduced by maternal (rearing or fraternal) environmental effects ($\hat{m}$) on litter size (Revelle and Robinson, 1973, Nelson and Robinson, 1976, Rutledge, 1980, Alsing, Krippl and Pirchner, 1980 and Van der Steen, 1983). While there is little doubt that these effects can be produced experimentally, there is some uncertainty about their importance under normal commercial conditions, specially with the widespread use of crossfostering practices in large breeding units. Indeed, some

indirect evidence questioning the relevance of maternal effects of the sort described comes from field data analyses. Relatively small $\hat{m}$ values would be expected to bias estimates of heritability from daughter on dam regressions, possibly giving negative estimates. It is likely that some negative estimates of heritability that are obtained go unreported. However, comparisons of heritabilities estimated from daughter-dam regression against paternal half-sib estimates give little evidence of bias. On the other hand, effects could be avoided by standardising litters at birth (Rutledge, 1980). Alternatively, if estimates of $\hat{m}$ were known with confidence, then records could be adjusted statistically for the size of the litter in which a female was reared. However, even if no adjustments were made, the relative efficiency of selection on the dams record alone would only be reduced to $(2/(2-\hat{m})$, or 0.95 for $\hat{m} = -0.1$, the literature average estimate. A similar conclusion was reached by Van der Steen (1983). The family selection index itself partially offsets such effects. By including information on many relatives the loss in efficiency with the full family index is approximately halved, so it would be 0.975 efficient.

The results of this thesis confirm the low value for the heritability of litter size in pigs. An overall estimate of 0.11 $\pm$ 0.01 was obtained here and this is the same as the average in the literature from analyses of large field data sets. The repeatability estimates were also similar to literature estimates. Among the genetic correlations of litter size between parities, only those for first and third or fourth parities deviated substantially from unity. More precise estimates are desirable but will be

difficult to obtain from field data analyses.

The experimental evidence for response to continuous selection for litter size in pigs is scarce. In particular, it has been pointed out that the disappointing results of Ollivier and Bolet (1981) are of limited value. It must be concluded that the best evidence available yet for the possibilities (and problems) of continuous selection for litter size in pigs comes from laboratory animals, and specially mouse experiments (reviewed by McCarthy, 1982). In this context, the positive results of Matheron (1982) continuously selecting rabbits on a family index to increase litter size are relevant. Whether this evidence across species is relevant is arguable. It is clear that pig experiments need to be designed in a large enough scale, both in numbers and duration. However, results from very intense selection of sows have given encouraging results. More importantly, these results fit in well with an additive genetic model for a quantitative trait. This gives some confidence in the parameters and in their use in predicting genetic responses from existing theory without need to invoke new principles. With regards to the use of family information, the theory is known to be robust (Sales and Hill, 1976).

The main theme of this thesis has been selection for litter size in pigs and some of the reasons for this have already been given. Although possible, on economic grounds it seems unlikely that anybody would want to select pigs continuously and exclusively for this trait. Were this to be the case, some notes of caution are needed regarding the size of herds required.

Clearly, with selection on parental records, the progeny of only two sows could replace all the boars needed for a 100 sow herd. This would have obvious consequences. Firstly, the sire family would hardly contribute information for selection (no variation between sires). Secondly, the rates of inbreeding would be very high, and as pointed out by Robertson (1961) and recently Burrows (1984), with selection on a family index, these rates may be much higher than those predicted by conventional formulae. Thus, either relatively large populations must be used or restrictions need to be imposed with the consequent reduction in achievable rates of response. Therefore, an analysis of the effects of using the family index proposed, on the accumulation of inbreeding is required. On the other hand, with inclusion of individual performance for growth and carcass traits the situation will tend to revert to one similar to mass selection.

Other reproduction traits, such as age at puberty, fertility, piglet survival and piglet litter weight, are also important economic objectives. More information is needed about the genetic parameters for these traits including genetic correlations among them, and with litter size and growth-carcass traits. If the genetic parameters were known, these would be included in the breeding objective (e.g. Smith, Dickerson, Tess and Bennett, 1983). Alternatively, rather than considering them individually in selection, some function of total weight of piglets per unit of age, or time, might be used (Bichard, 1983a) but this would tend to emphasise the most variable component.

Several alternatives are open to the breeder wishing to select for litter size in pigs. The hyperprolific selection system

can be a useful way to set up a nucleus herd from a previously unselected population, but not for achieving high and continuous response. If genetic lag for other traits is a concern, it is advisable to increase accuracy of selection by using family records rather than increasing the number of records on individuals. However, it has been pointed out that selection on the mean of four records might not be the same trait as litter size, since longevity, fertility and other traits contribute to the former (Bichard, 1985 personal communication). High rates of response can also be obtained with progeny testing of males from a nucleus herd, on a large recorded population of females bred by AI. However, when all economic traits are considered, including growth and carcass traits, neither the hyperprolific scheme nor the progeny testing system are likely to match the overall economic response from selection in a combined family selection index of the type described here.

The general conclusion about the low to moderate value of including litter size in a selection index, agrees to some extent, with previous work both in the UK (Clarke and Smith, 1979) and in USA (Smith et al., 1983). Despite the high rate of response possible by selecting for litter size on its own, the effects of the economic weights and higher heritabilities of the other traits accumulate to reduce the value of litter size in the overall index, as pointed out by Smith (1983). However the economic loss from ignoring litter size with full family information from an index for specialised dam lines is estimated to be as much as 20%.

The possibility of using family information for litter size selection in pigs had received little attention previously,

even though Hill and Webb (1982) had commented briefly on the possibilities. More recently, Schinkel (1985, personal communication) has developed indices making full use of family information. Whatever the reasons for not making previously use of family information, clearly in the future this method of selection shall make an impact in pig breeding in at least two ways:

1. Changing the current thinking about rates of response considered possible for litter size in pigs.
2. Partly as an extension of the first point, and including other reproductive traits (also lowly heritable but variable, like fertility), the use of family information in indices will probably justify, for the first time, effective specialisation in sire and dam lines.

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APPENDICES

APPENDIX A1.1

Changes with time of the relative contribution per standard deviation improvement in individual reproductive components on overall sow productivity (pigs/sow/year).

Number of reproductive cycles	1	2	3	4	5
Component					
Age at first farrowing (%)	12	8	6	5	4
Rebreeding intervals (%)	0	5	8	10	12
Litter size (%)	30	30	30	30	30

Constants used and derived parameter

Constants (assumptions)	$\bar{x}$	σ_p
Age to first farrowing	330	35
Rebreeding interval	40	25
Litter size	10	3

Derived parameters					
Number of reproductive cycles	1	2	3	4	5
Age at farrowing	330	485	640	795	950
Litters/sow/year	1	1.3	1.7	2.2	2.6

APPENDIX A2.1

Analysis of variance for repeatability (t) estimates of rebreeding intervals.

Lactation length	Variable		Constant	
Breed	Landrace	Large White	Landrace	Large White
Degrees of freedom				
Females	1568	1756	1568	1756
Residual	1666	1900	1664	1898
Mean squares				
Females	1069.8**	747.0**	1067.4**	745.2**
Residual (σ_W^2)	623.00	557.70	611.50	540.50
Coefficient (k)[1]	2.03	2.05	2.03	2.05
Estimates				
Component (σ_B^2)	220.60	92.50	225.30	100.50
t	0.26±0.02	0.14±0.02	0.27±0.02	0.16±0.02

[1] Coefficient for σ_B^2

$t = \sigma_B^2/(\sigma_B^2 + \sigma_W^2)$

** $P<0.01$

APPENDIX A2.2

Analysis of variance for repeatability (t) estimates of litter size.

Breed		Landrace	Large White
Degrees of freedom			
Females		2360	2450
Residual		3288	3711
Mean squares			
Females		10.51**	12.53**
Residual	(σ_W^2)	8.21	8.25
Coefficient	(k)[1]	2.36	2.48
Estimates			
Components	($\sigma_B 2$)	0.97	1.73
t		0.11±0.02	0.17±0.02

[1] Coefficient for σ_B^2

$t = \sigma_B^2/(\sigma_B^2 + \sigma_W^2)$

** P<0.01

APPENDIX A2.3

Combined analysis of variance for heritability estimates from half-sib and full-sib families. Gilt litter size.

Source	Degrees of freedom	Mean squares Numbers born total	Mean squares Numbers born alive	Expected mean square
Between sires (within breed)	554	8.09	8.23	$\sigma^2_W+k_2\sigma^2_D+k_3\sigma^2_S$
Between dams	2838	7.05	7.02	$\sigma^2_W+k_1\sigma^2_D$
Residual	1417	6.88	6.88	σ^2_W
Heritability (h^2)		0.07±0.05	0.08±0.06	

Coefficients:

$k_1 = 1.37$, $k_2 = 1.67$, $k_3 = 8.64$

$h^2 = 4\ \sigma^2_S/(\sigma^2_S + \sigma^2_D + \sigma^2_W)$

APPENDIX A2.4

Analysis of variance for heritability estimates from separate groups of paternal half-sibs. Gilt litter size.

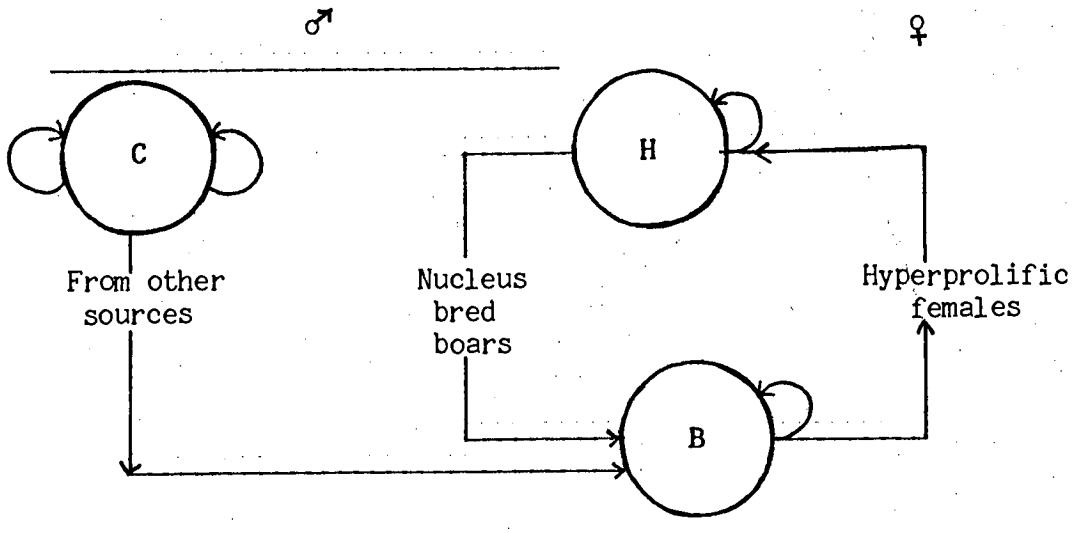
Breeds	Landrace		Large White	
Groups	1st	2nd	1st	2nd
Degrees of freedom				
Sires	285	285	269	268
Residual	1372	1372	1461	1472
Mean squares				
Sires	7.45	7.50	7.97	8.65
Residual (σ_W^2)	6.57	6.85	6.91	7.13
Coefficient (k)[1]	5.79	5.78	6.40	6.46
Estimates				
Component (σ_S^2)	0.15	0.11	0.16	0.23
Heritability (h^2)	0.09±0.07	0.06±0.07	0.09±0.06	0.12±0.07

[1] Coefficient for σ_S^2

$h^2 = 4\,\sigma_S^2/(\sigma_S^2 + \sigma_W^2)$

APPENDIX A5.1

Gene flow diagram for continuous 'hyperprolific scheme' and condensed matrix **P** for gene flow methods. Cases 2 and 3.



H - Hyperprolific Nucleus
B - Base population
C - Commercial nucleus boars

Paths of gene flow (Blocks in **P** matrix)

H males to H	C males to H	B females to H
H males to B	C males to B	B females to B

Case 2: 1/3 of sows in B mated to boars from H

$$\tilde{P} = \left[\begin{array}{cc|cc|cccccc} 0 & 1/2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1/2 \\ 0 & 1/6 & 0 & 2/6 & 0 & 1/4 & 1/8 & 1/16 & 1/16 & 0 \end{array}\right]$$

Case 3: 1/6 of sows in B mated to boars from H

$$\tilde{P} = \left[\begin{array}{cc|cc|cccccc} 0 & 1/2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1/2 \\ 0 & 1/16 & 0 & 7/16 & 0 & 1/4 & 1/8 & 1/16 & 1/16 & 0 \end{array}\right]$$